AFRL-AFOSR-UK-TR-2012-0029

Multisensory Control of Stabilization Reflexes

Professor Holger G. Krapp

Imperial College of Science and Technology
Department of Bioengineering
South Kensington Campus
London, United Kingdom SW7 2AZ

EOARD Grant 09-3022

Report Date: August 2012

Final Report from 01 November 2008 to 01 May 2012

Air Force Research Laboratory
Air Force Office of Scientific Research
European Office of Aerospace Research and Development
Unit 4515 Box 14, APO AE 09421

REPORT DOCUMENTATION PAGE

Form Approved OMB No. 0704-0188

1. REPORT DATE *(DD-MM-YYYY)*	2. REPORT TYPE	3. DATES COVERED *(From – To)*
22 August 2012	Final Report	1 November 2008 – 1 May 2012

4. TITLE AND SUBTITLE

Multisensory Control of Stabilization Reflexes

5a. CONTRACT NUMBER

FA8655-09-1-3022

5b. GRANT NUMBER

Grant 09-3022

5c. PROGRAM ELEMENT NUMBER

61102F

6. AUTHOR(S)

Professor Holger G. Krapp

5d. PROJECT NUMBER

5d. TASK NUMBER

5e. WORK UNIT NUMBER

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

Imperial College of Science and Technology
Department of Bioengineering
South Kensington Campus
London, United Kingdom SW7 2AZ

8. PERFORMING ORGANIZATION REPORT NUMBER

N/A

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)

EOARD
Unit 4515 BOX 14
APO AE 09421

10. SPONSOR/MONITOR'S ACRONYM(S)

AFRL/AFOSR/RSW (EOARD)

11. SPONSOR/MONITOR'S REPORT NUMBER(S)

AFRL-AFOSR-UK-TR-2012-0029

12. DISTRIBUTION/AVAILABILITY STATEMENT

Approved for public release; distribution is unlimited.

13. SUPPLEMENTARY NOTES

14. ABSTRACT

Besides the academic outputs produced during the period of funding – and probably beyond – one of the most important outcomes over the last couple of year has been a clear research agenda for this work. While collaborating with the groups of Graham Taylor and Sean Humbert this research has shaped into a system neuroscience approach that combines quantitative behavior, electrophysiology, functional anatomy and modeling to advance our understanding of biological control design – with a strong emphasis on the underlying neuronal mechanisms. In particular the interactions with Sean Humbert have resulted in several tangible outputs, e.g. the proof of concept study showing that LPTC receptive fields can be successfully used to control orientation, proximity and forward speed of a quadropter (O35) or the development of an ocellar senor (C6). Future interactions between the group and the groups of collaborators will aim to further discover and exploit biological design principles in the context of control and navigation of autonomous robotic systems. The emphasis will be to advance autonomy and manoeuvrability by multisensor fusion, dynamic range fractioning and the integration of inner- and outer loop control.

15. SUBJECT TERMS

EOARD, Flight Control, Insect Vision

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18, NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT	b. ABSTRACT	c. THIS PAGE			Gregg Abate
UNCLAS	UNCLAS	UNCLAS	SAR	38	19b. TELEPHONE NUMBER *(Include area code)* +44 (0)1895 616021

USAF Grant FA8655-09-1-3022 ` **Holger G Krapp**

Department of Bioengineering email: h.g.krapp@imperial.ac.uk
Imperial College
South Kensington Campus
London SW7 2AZ

"Multisensory Control of Stabilization Reflexes"

(Period of finding: October 2008 – September 2011)
NCE March 2012

Final Technical Report

Contents:

1. General Summary of Achievements.

Grant FA8655-09-1-3022, "Multisensory Control of Stabilization Reflexes", provided general funding for research in my lab. It covered the salary of one of my senior research associates (RA), Dr. Kit Longden, who works on energy efficient, state-dependent coding of self-motion information (see below). Kit is now funded from another grant with AFOSR/EOARD which I am holding (FA8655-09-1-3083) together with Dr. Sean Humbert (FA9550-09-1-0075), University of Maryland on the integration of compound eye and ocellar signals for gaze and flight control. In this final report I will stick with the tradition I previously introduced to include related developments and progress on (a) all Air Force-funded research activities and (b) most if not all projects supported by other funding agencies. As a result, some of the material I include here may also be presented in other reports submitted by my collaborators or by myself.

1.1 Publications

When I submitted my last report two journal articles (O35-36) and a book chapter (R4) were only submitted but have now been successfully published. In 2011/2012 another four papers in peer reviewed journals came out: on multisensory integration in the fly neck motor system (O37), on (fly)brain-machine interfacing (O38), on state-dependent processing in lobula plate tangential cells (O39) and another one in Journal of Neuroscience (O40) on behavioural and electrophysiological responses of flies to "plaid" stimuli (superimposed visual gratings) in combination with phenomenological modelling of the motion vision pathway.

Total number of publications within the funding period directly or indirectly supported by AFRL/AFOSR/EOARD:

- **12** publications in peer reviewed journals (O28-36, O38-40)
- **4** peer reviewed conference papers (C3-C6)
- **1** book chapter (R4)
- **17** conference abstracts (A38-54)

In addition we are currently working on at least 4 further scientific publications relevant to the subject area of this grant where the manuscripts are either almost ready for submission (O41-42) or where the data have been analyzed and we are currently writing up the results (O43-44).

1.2 Scientific Workshops, Conferences, and Seminars

From October 2010 until today I was invited to 8 international workshops and conferences including **(i)** an ESF-EMBO-funded symposium on *"Neurobiology in Minibrains: From flies to robots, and back again"*, Sant Feliu de Guixols, Spain, (2010), **(ii)** a topical conference on *"Fly Vision"* at the Howard Hughes Medical Institute, Janelia Farm Campus, Washington DC, USA, (2011), **(iii)** the 4th annual workshop on *"Bio-inspired control design"* at the Air Force Research Laboratory, Eglin, FL, USA, (2011), **(iv)** a cross-Atlantic topical meeting on *"Bio-MAV SOAR"* at Chilworth Manor, UK, supported by the Air Force Office of Scientific Research, USA & Defense Science and Technology Laboratory, MoD, UK (2001), **(v)** a congress on *"Flow sensing in air and water"*, at the University of Bonn, Germany, where I presented the ***public plenary lecture*** of the event (2011), **(vi)** the 5th annual workshop on *"Bio-inspired control design"* at the Air Force Research Laboratory, Eglin, FL, USA, (2012), **(vii)** a conference on *"Bioactive Amines"*, Freie Universität Berlin, Germany, where the talk was presented by Dr. Kit Longden (2012), and **(viii)** the 1st conference on Biomimetic and Biohybrid Systems, *"Living machines"*, Barcelona, Spain, (2012). I was also invited to give seminar talks at **(a)** the University of Tübingen, Germany, (2010), **(b)** the University of Newcastle, UK, (2011), and **(c)** the Heriot-Watt University, Edinburgh, UK, (2012).

Total number of invitations to scientific workshops, conferences and seminars within the funding period:

- **17** invitations to present at international scientific conferences
- **5** national and international invitations to give a seminar talk

Next year I have been invited to attend 4 international conferences. One will take place in London where I will act as local co-organizer (see below) and another one where I will be presenting a plenary lecture. Kit Longden was invited to present his work on state-dependent processing in the fly motion vision pathway at two conferences this year. He was presenting at a topical conference on bioactive amines in Berlin (see above) and at the ISN meeting, University of Maryland, as one of the speakers in a dedicated symposium (see below). Kit has also been invited to give two oral presentations at conferences next year.

1.3 Poster and Oral Presentations at National and International Conferences

This year members of my group will present 3 posters at the International Congress of Neuroethology (2012, University of Maryland, USA) and 2 posters at the European Microscopy Congress (2012, Manchester, UK). At both conferences one of our contributions will be an oral presentation (cf. A50-54).

From 2010-2011 we presented another 6 posters at international meetings (cf. A44-49).

Total number of poster and oral presentations within the funding period:

- **17** conference abstracts (A38-54; cf. above)

1.4 Funding

Current funding secured for research in my laboratory (excluding FA8655-09-1-3022):

- **HFSP** research collaboration, PI, with three other PIs: Drs. Manos Drakakis, Imperial College, Fabrizio Gabbiani, Baylor College of Medicine, TX, USA, Martin Egelhaaf, Bielefeld Universty, Germany: *"Comparative analysis of RF-transmitted neural activity on flying insects."* [***Non cost extension until end of September 2012***]

- **AFOSR**, through EOARD, PI, together with Dr Sean Humbert, PI University of Maryland: *"The relationship between visual sensor equipment in flying insects and their flight performance – a 'Neurobio-Engineering' approach."* [***Funding for work in my lab until end of September 2013***]

- **Wellcome Trust** research grant, PI: *"Integrated reflex control" in Manduca.* [***Funding until end of April 2014***]

- **DSTL-sponsored EPSRC Industrial CASE PhD Studentship**, PI: *"The significance of (image) gaze stabilization - Comparative studies on gaze control design in flying insects using behavioural, computational, and electrophysiological techniques."* [***Funding until end of March 2015***]

- **DSTL National PhD Programme**, PI: *"The significance of (image) gaze stabilization - functional characterization of the neck motor system using electrical stimulation of identified neck muscles in blowflies."* [***Funding until end of September 2016***]

Grant proposals submitted:

- **AFOSR/EOARD**, PI, together with Dr Graham Taylor, PI, University of Oxford, UK, and Dr Sean Humbert, PI, University of Maryland: *"The mode sensing hypothesis"* [***Decision pending***]

- Seventh Framework Programme (FP7) with the European Commission. Co-PI on an international consortium of neuroscientists, engineers, theoreticians from the UK, Germany, and Switzerland on *"ChemXplore – visually-guided exploration of chemical landscapes."* My part will include experimental and modelling work on a multisensory (vision-olfaction) control design for autonomous micro-air-vehicle application. [***Invited to submit full proposal***].

Grant proposals in preparation:

- We are currently preparing the full FP7 *ChemXplore* proposal which is highly relevant in the context of micro-air-vehicle, guidance, navigation and control. To my knowledge, there is no aerial robotic system, so far, that combines visual and olfactory information for GNC.

1.5 Group size, Collaborations, and Scientific Impact

Group size*:*

My group currently consists of 2 RAs (postdocs) and 4 postgraduate students. In addition I currently supervise 4 MSc project student and 4 UG summer internship students. I also co-supervise a DSTL-funded DPhil student together with Graham Taylor at the University of Oxford. Should the current grant application with AFOSR/EOARD be successful I will employ another RA. I am also looking into funding opportunities for more PhD students as two of my current PhD students will submit their theses within the next few months.

Collaborations*:*

At Imperial College I am collaborating with several groups in the Department of Bioengineering: Dr Martyn Boutelle (Biosensors), Dr Simon Schultz (Neural Coding), Dr Manos Drakakis (Low-power VLSI technology), and Dr Reiko Tanaka (Compound Control). To study the functional anatomy of insects we still collaborate with the micro-CT group at the Natural History Museum, London. More recently, we have also started to collaborate with scientists at the Paul Scherre Institute, Swiss Light Source, Switzerland, to obtain high-resolution 4D data from tethered flying flies on the functional organization of their fight and neck motor systems. Collaboration with Prof Simon Laughlin (Cambridge) and Dr Graham Taylor (Oxford), have been maintained and will be intensified by means of joint grant applications. International Collaborations include work with Prof Martin Egelhaaf, Neurobiology, Bielefeld University, Germany; Prof Fabrizio Gabbiani, Baylor College of Medicine, USA; Prof Sean Humbert, Department of Aerospace Engineering, University of Maryland, USA; and Mr Ric Wehling at the AF Research Laboratory, Eglin, US.

***Bibliometric Data and Scientific Impact**:*

Bibliometrics:

	Nov 2008	Aug 2012
Number of publications*	27	46
Number of citations**	753	1619
h-factor**	16	23

* = including reviewed conference proceedings, excluding book chapters
** = according to *"Harzing's Publish or Perish"*

Over the funding period (October 2008 until end of March 2012) there has been a significant increase of scientific outputs and impact regarding the number of both publications and citations.

Scientific Impact:

- ***Refereeing manuscripts*** for more than 30 peer review journals, including *Nature*, *Science*, and *Neuron*.
- ***Refereeing grant applications*** for 9 funding agencies including *RCUK*, *NSF (USA), and AFOSR (USA).*
- ***Expert Reviewer*** for *European Commission FP7* collaborative project
- Member of ***Academic Editorial Board*** *of open access journal* ***PLoS ONE***
- ***Financial Co-organizer*** AFOSR/DSTL "*Bio MAV SOAR*" meeting, Chilworth Manor, 2011 and UK follow-up meeting at Imperial College, London, 2012.

- Member of ***Programme Committee*** of Conference on *Biomimetic and Biohybrid Systems* "Living Machines", Barcelona, 2012

- ***Co-ordination*** of DSTL-supported virtual *Centre of Excellence* on Unmanned Autonomous Systems (*UAS – former "MAV"*) with meetings at Imperial College, Feb 2012, and at the University of Oxford, Aug 2012

- ***Local Co-organizer*** of Conference on *Biomimetic and Biohybrid Systems* "Living Machines", London, 2013

- ***Co-applicant/proposer*** of research call initiatives in the area of sensing and actuation (ESF/NSF) and *"Robot Companions"*, Flagship proposal submitted to the European Commission.

In parallel with the increase of my bibliometric outputs, I have also taken on more responsibility in terms of (i) fostering visibility and promote areas relevant to the remits of AFRL/AFOSR support and (ii) contributing to a high standard in conducting scientific research by expanding my commitment to reviewing and editorial work.

2. Report on current projects:

My scientific interest focuses on the neural mechanisms underlying the control of behaviour. In my lab we perform comparative studies on sensorimotor control in flying insects which are based on a systems neuroscience approach. We aim to discover general principles and species-specific adaptations regarding the relationship between morphological structures, neural information processing and motor control. Most of my previous research focussed on visuomotor control in blowflies and locust. To identify general principles of sensorimotor control I have recently included several other dipteran flies and moths (*Manduca sexta*) as experimental model systems. Together these model systems show a sufficiently large degree of diversity to extract specific adaptations and common functional principles in terms of how behaviour, morphology, and neuronal processing and motor control are linked together.

Over the funding period of this project, I have been developing four complementary research priorities which are meant to advance our understanding of the neural basis of biological control design and its translation into technical applications. These research priorities include:

2.1. ***Behavioural performance*** of multisensory motor control in dipteran flies
2.2. ***Biomechanics of motor systems***
2.3. ***Neural mechanisms*** underlying multisensory motor control in dipteran flies
2.4. ***Modelling*** of multisensory motor control design

In the following I will report progress on these research priorities which are funded by AFRL/AFOSR, HFSP, Wellcome Trust, DSTL and Imperial College resources, or are continuations/expansions of collaborations based on previous funding.

2.1. ***Behavioural performance*** of multisensory motor control in dipteran flies

In previous reports I emphasised the significance of gaze stabilization for the stunning aerodynamic capabilities of dipteran flies. In particular bigger species where inertial forces have a significant impact on the animal's flight dynamics strongly rely on gaze stabilization to (a) reduce motion blur and to (b) establish and maintain a common frame of reference relative to the inertial vector for head-based sensor systems such as antennae, compound eye and ocelli. Because the neck motor system of an insect initiates compensatory head movements whenever the body changes orientation due to external disturbances or voluntary trajectory changes – gaze stabilization is intimately linked to flight stability and control.

We have performed quantitative behavioural experiments, over the last couple of years, using a linear systems analysis approach to characterize the dynamic responses of the fly gaze stabilization system within a control engineering framework (O37). One of the most important properties of fly gaze and flight control is that they rely on signals from a wide variety of sensor systems (O24). According to studies by Hengstenberg (e.g. rev.: 1993) in the velocity domain, signals from different sensor systems are internally scaled and are then linearly combined to control compensatory head movements. Earlier anatomical (Strausfeld et al. 1987) and electrophysiological (Wertz et al. 2007) work supports the idea that those signals are simply added in descending neurons by employing electrical synapses. On the other hand, there is evidence that some neck motor neurons involved in gaze stabilization have highly non-linear signal integration properties in that they only generate action potentials when receiving input from at least two different sensors (e.g. O30).

To guide our studies on the neural mechanisms underlying multisensory gaze and flight stabilization, we performed a couple of behavioural experiments on compensatory head roll in *Calliphora* where we systematically manipulated the combination of sensor systems contributing to the response. Head roll was monitored using a high-speed video camera while the animal was subjected to sinusoidal stimulation of various sensors to obtain the respective frequency response. From the frequency responses under closed-loop conditions we derived transfer functions which, in turn, could be used to set up a simulation platform for fly gaze stabilization (see also below). We chose a linear systems analysis approach. This was justified by two-tone modulation experiments, where the sum of two stimulation frequencies only produced small contributions of higher harmonics in the behavioural response – which suggests a *mostly* linear system (O37).

There are two sets of fundamental questions regarding multisensory reflex control: Firstly, what is the design of the control architecture underlying gaze and flight stabilization? More specifically, how are visual, mechanosensory and proprioreceptive signals – measured by head- and thorax-based sensors (O24) – combined in the feedforward and/or feedback sense to provide reasonably robust motor commands? Secondly, how are the responses – each of which incurs a pathway- specific response delay – amplified/attenuated to enable a sufficiently large bandwidth without compromising stable control? In this context it should be particularly interesting to review the motion vision pathway supplied by the compound eye. In light-adapted flies, motion vision is primarily (70%) based on a spatio-temporal correlation of light levels measured in adjacent ommatidia within the

hexagonal eye lattice. The spatial sampling base determined by the interommatidial angle between neighbouring facets in combination with the time constant in the elementary movement detect (rev.: O24) results in a optimal response of the system to pattern motion in the range of hundreds of degrees per second (rev.: e.g. Hausen 1993). Why does the system not employ motion detectors with larger sampling bases to shift its maximum sensitivity to higher angular velocities by, for instance, including next-but neighbouring ommatidia? A tentative answer may come from the fact that the response delay in the motion vision pathway is rather long due to the extra time required to compute directional motion. Just increasing gain and bandwidth but leaving the response delay unchanged potentially bears the risk of instabilities in a closed-loop feedback system.

Our previous and recent experiments on *Calliphora* compensatory head roll addressed these two sets of questions focusing on the architecture and stability of the control system (O37, O41).

We performed experiments where the compensatory head roll was measured in animals whose thorax was oscillated by +/- 40 degrees and at different frequencies for two conditions: C1 = stimulating the compound eye motion vision pathway and the halteres, and C2 = only stimulating the compound eye motion vision pathway. The results suggested that signals obtained by these two major sensor systems are combined according to an architecture that is known in engineering as *two degrees of freedom controller*: One control degree is provided by the halters which mediate a feedforward response that results in an initial compensatory head roll. This fast response component effectively reduces the remaining retinal slip speed to a velocity range the motion vision pathway is most sensitive to. The second control degree corresponds to negative feedback provided by the motion vision pathway in an attempt to compensate for the remaining retinal slip speed. The fast response component initiated by the halteres, in a way, linearizes the system as it shifts the distribution of retinal slip speeds into the operating range of the motion vision pathway (O37, O41). The methodology used and results obtained are presented in Figures 1-3 (Schwyn et al., in prep, O41).

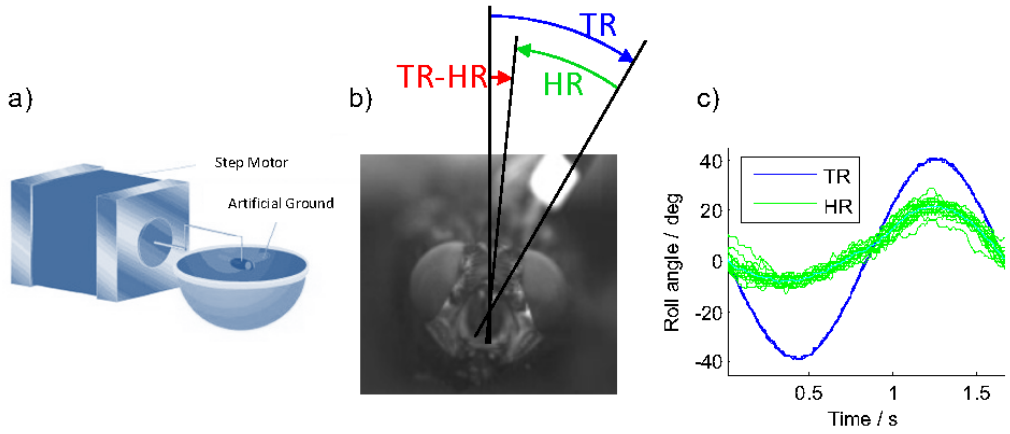

Figure 1: Experimental setup (a) and analysis (b) of compensatory head roll (HR) during externally forced thorax rotations (TR). The performance of the neck motor system is reflected by the difference HR-TR. Perfect compensation for TR would result in HR = 0. (c) TR and HR are shown as a function of time. (from Schwyn et al. in prep, O41).

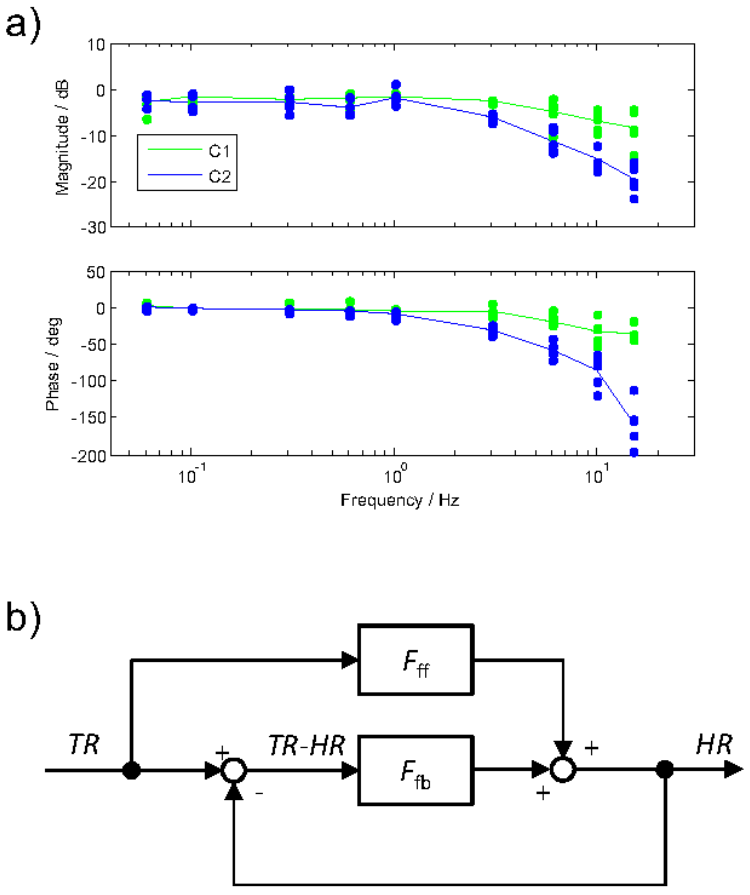

*Figure 2: **(a)** Bode plot of frequency responses of Calliphora compensatory head roll for thorax oscillation amplitudes of +/- 40 degrees. C1 and C2 refer to stimulation of the motion vision pathway with and without the halters being intact, respectively. Note that without halters the roll off frequency is shifted to lower stimulation frequencies. N=4 different flies. **(b)** Two degrees of freedom controller. The forward component is provided by the thorax-based halteres which initiate a fast compensatory head roll. The remaining retinal slip speed, i.e. the relative motion between the compound eyes and the fixed visual environment, is then sensed by the motion vision pathway which generates the 2nd degree of freedom of the controller mediating a negative feedback signal. (From Schwyn et al., in preparation, O41).*

From the results shown in Fig. 2, the open-loop pathway transfer functions can be calculated (Fig. 3c), which in turn are used to assess the stability margins of the motion vision pathway in combination with the neck motor system. The rational of focusing on the feedback degree of freedom of the control architecture shown in Fig. 2b is that the slowest component on its own is required to perform in a stable way for the entire controller to be stable.

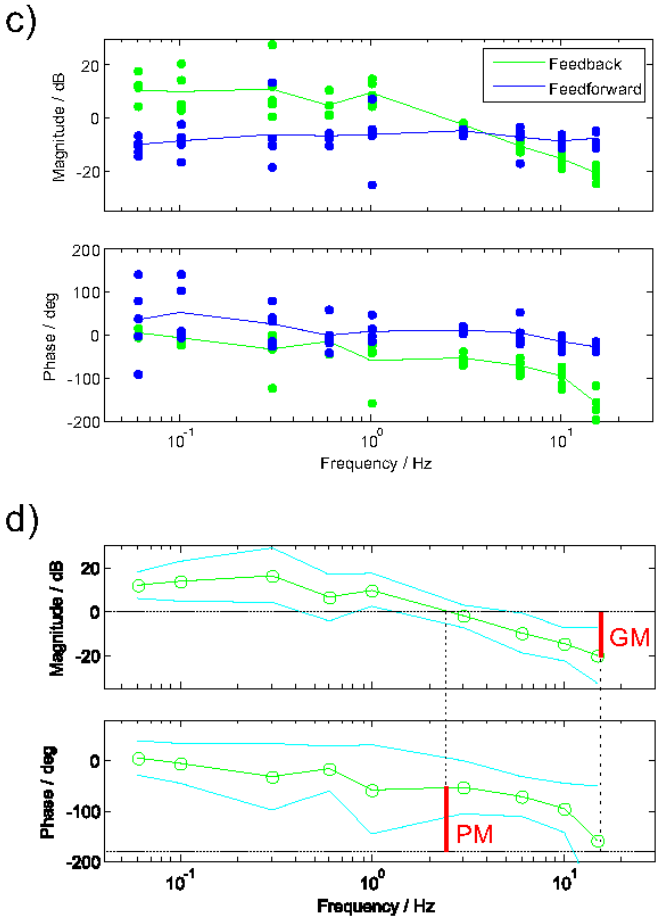

Fig 3: ***(c)*** *Open-loop transfer function for the feedback (green) and feedforward (blue) components of the 2 DoF controller, respectively.* ***(d)*** *Stability margins for the open-loop pathway transfer function involving the motion vision pathway. Note the surprisingly high gain (upper plot, GM) and phase (lower plot, PM) margins, respectively. Green circles give the mean values obtained from four animals with magenta lines indicating the standard deviation. (from Schwyn et al., in prep, O41).*

Surprisingly, our analysis of the transfer function including the motion vision pathway indicated unexpectedly high stability margins. The gain margin (Fig. 3d, GM) at the 180 degrees phase reversal is still 20 dB, and the phase margin at the zero-crossing in the gain plot amounts to 130 degrees (Fig. 3d, PM).

Given these values, the motion vision pathway seems to be totally stable and could even accommodate longer fixed response delays without risking instable performance. Why is there so much leeway build into the controller? Our interpretation is that, by implementing extra high stability margins, the control system can cope with a large amount of variability – or noise – inherent to each of the individual sensory pathways. Noise distributions in different sensor systems may have different shapes, which could mean that even if the sources are independent they may not cancel out each other. Also, expansive non-linear processes when combining signals from different modalities could potentially boost the feedback signals beyond a magnitude that is

tolerable for stable control. Further studies, specifically aiming to reveal potential non-linearities in multisensory integration are on its way (See next paragraph).

As mentioned above, signals from different sensors may be combined in a non-linear way. One example would be the gating effect in neck motor neurons observed during compound eye and haltere stimulation. An exciting question to ask is: given the non-linear processing steps in the motion vision pathway and other neural processing stages known to affect sensory integration (O28, O32), how does the system manage to produce an overall fairly linear behavioural output? Obviously, for each non-linear process there should be another non-linear process that roughly compensates for it.

We have now started to perform behavioural experiments to study the combination of specific sensor systems, for instance the interaction between the compound eye and the ocellar pathways – a project highly relevant in the context of the joint research grant (FA8655-09-1-3083) together with Dr Sean Humbert, UMD. Previous electrophysiological work has shown that the impact of the ocellar system on the motion vision pathway can be observed at the level of lobula plate tangential cells (O20, O36) – probably due to electrical synapses connecting to descending neurons which integrate signals from several sensory systems.

Our experiments were performed on tethered flying animals in a static position. To stimulate the motion vision and ocellar systems we oscillated a dark hemisphere in the ventral visual field at different frequencies and amplitudes. The stimuli mimicked a rotation of the animal round the roll axis. Two conditions were tested: compound eye + ocellar and only compound eye stimulation (painting over the ocelli), respectively.

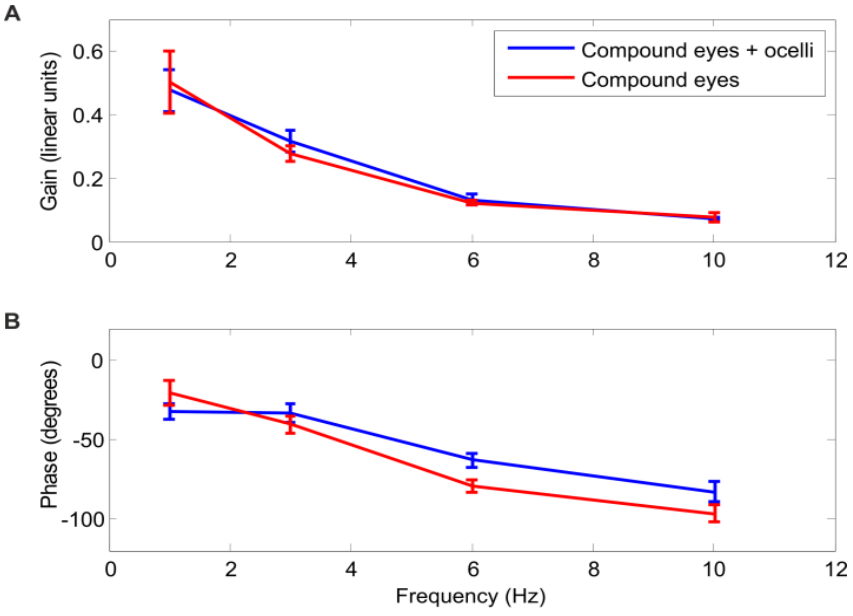

Figure 4: A) Gain and B) phase of open-loop head roll responses in tethered flying flies during +/- 30 degree oscillation of a black ventral hemisphere plotted against stimulus frequency. Red and blue curves give responses in flies with and without ocellar input. Note that the ocellar input does not affect the gain but reduces the phase delay for responses to frequencies above 3 Hz. Mean values of N=7 flies +/- SEM. Schwyn et al., work in progress.

Interestingly, the gain did not depend on whether or not the ocelli contributed to the response (Fig 4). The phase, however, was advanced, when the ocelli were stimulated

in addition to the compound eyes. This result, compatible with previous electrophysiological studies (O36), indicates a non-linear integration of compound eye and ocellar signals at the descending neuron level. As pointed out in previous publications (e.g. O36, Elzinga et al. 2011) closed-loop feedback control in biological systems heavily relies on short response delays to prevent instabilities. The behavioural data (Fig. 4) show that the combination of compound eye and ocellar signals mainly achieves a shorter response delay without increasing the gain. This finding could be interpreted as evidence that reducing response delays in pathways mediating negative feedback signals might indeed be a fundamental aspect of multisensory integration in biological control systems.

A potential mechanistic model which may explain those results would include a static threshold non-linearity as presented in figure 5 (A50). Including another level of modelling – here mechanistic in addition to phenomenological – will be required to incorporate neural mechanisms of multisensory signal integration as a complementary approach to a systems analysis/identification adapted from engineering.

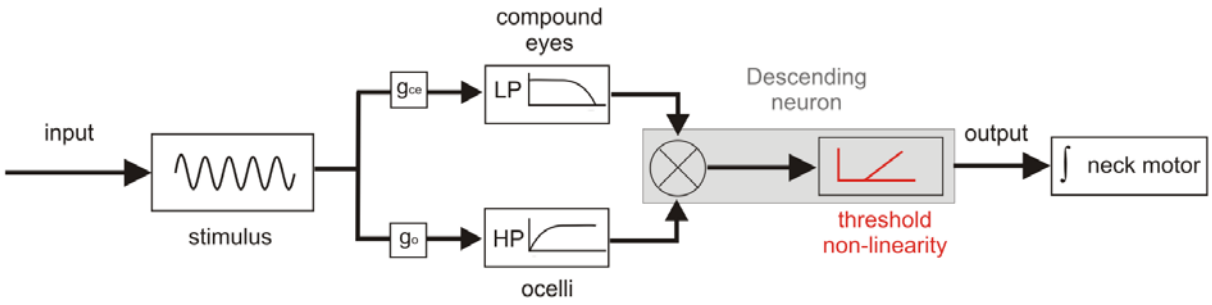

Figure 5: mechanistic model of non-linear combination of compound eye and ocellar signals at the level of a descending neuron. This simplified model approximates the transfer functions of the compound eye-mediated motion vision pathway and the ocellar pathway by 1st order low-pass and high-pass filters, respectively, in combination with individual pathway gains. The output of both visual systems is integrated by a descending neuron that converts membrane potential changes into trains of action potential through a static threshold non-linearity. The model captures the experimental result that ocellar signals do not increase the overall gain along the combined pathway but reduce the phase shift of the response. (work in progress).

In conclusion, over the funding period of this grant we have performed a number of behavioural studies to evaluate gaze stabilization behaviour in *Calliphora* within a control engineering framework. Using a linear systems approach to start with, we were able to propose a controller design (two degrees of freedom) that combines mechanosensory feedforward with visual feedback signals. We also demonstrated the presence of non-linear processes, probably at the level of the descending neurons, in the context of compound eye and ocellar signal integration.

Our results seem to be in contradiction with electrophysiological studies suggesting a linear combination of compound eye and ocellar signals. However, the nature of a threshold non-linearity as proposed in the block diagram in Fig 5 does not exclude a linear combination of inputs once the threshold potential for triggering action potentials is reached. Beyond the threshold potential, inputs may result in a linear

increase of the descending neuron's spike rate with increasing signal amplitudes mediated by the compound and ocellar systems. Similarly, sub-threshold inputs may indeed add up linearly as demonstrated by Haag et al. (2007) in recordings from ocellar L-neurons, LPTCs and descending neurons. Sub-threshold activity changes, however, would not result in any behavioural output as the latter requires the generation of action potentials to induce muscle contraction via motor neurons. Further experiments will be needed to pinpoint the exact mechanism underlying ocellar and compound eye signal integration.

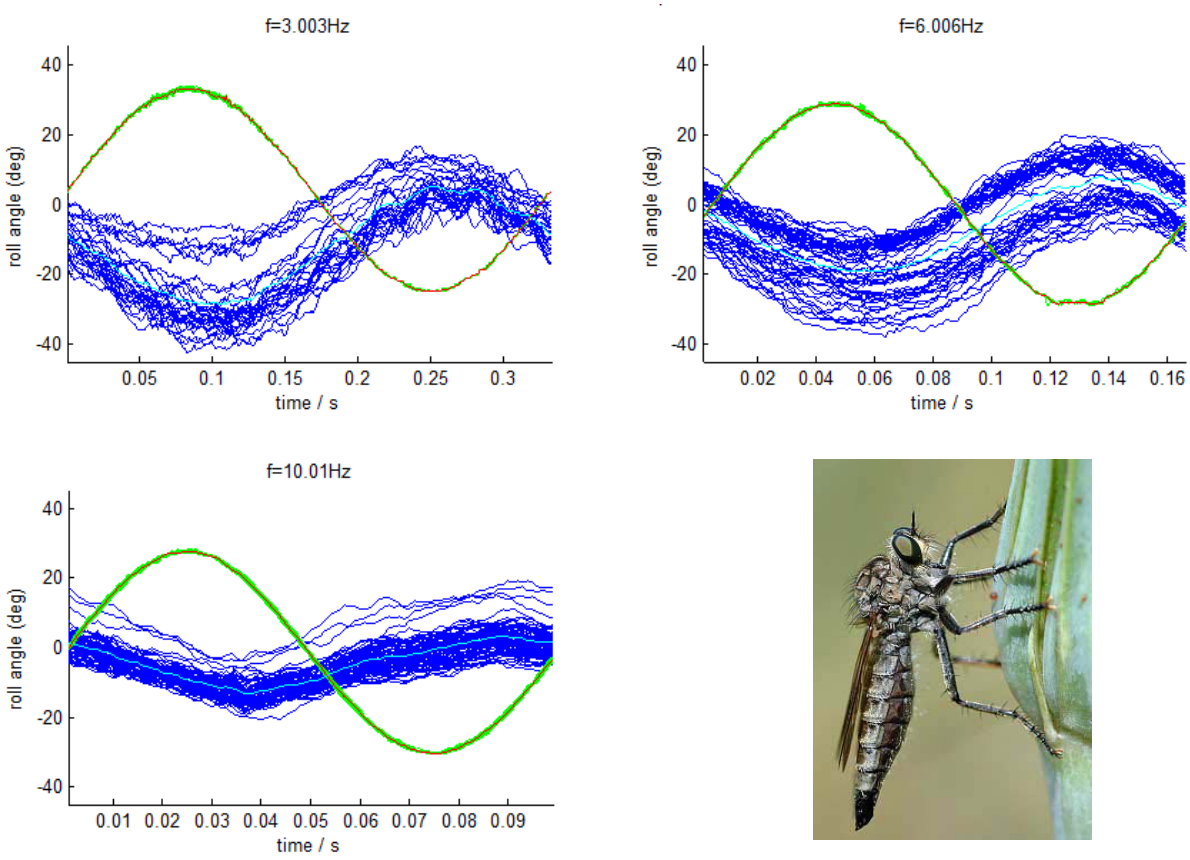

Figure 6: Roll gaze stabilization in the robberfly (Dysmachus spec.) at different thorax oscillation frequencies. Green and blue traces show the stimulus and compensatory head roll movements over time, respectively. Note that in this case the blue trace indicates the action of the neck motor system. Bottom right: Dysmachus Spec. Source: Geller-Grimm (A53, Hardcastle et al. work in progress.)

We have also begun to perform gaze stabilization experiments in dipteran species other than *Calliphora*. First experiments on a UK robberfly species (*Dysmachus spec*, Fig. 6) and on hoverflies (*Eristalis spec*) suggest that both these animals also perform compensatory head roll movements when subjected to thorax rotations.

Two exciting results are: (a) robberflies do show head roll responses independent on whether or not they are flying – i.e. wing beat generation is not a necessary condition

for compensatory head roll to occur as it is for *Calliphora* and (b) hoverflies, which were thought not to perform compensatory head roll responses at all (Collett and Land, van Hateren lab), did in fact show head roll responses under the experimental conditions we applied, at least in some cases. It is likely that previous work on hoverfly head roll was suffering from a sampling bias, i.e. many hoverflies do not show head roll but some actually do. A bimodal distribution of animals, part of which did perform head movements while the other part did show a near-zero gain had been reported for blowflies by Rosner et al. (2009).

2.2. *Biomechanics of motor systems*

Up to a certain degree – systems analysis approaches in a linear control engineering framework have been successful to provide phenomenological models of the overall performance in stabilization behaviours. However, they do not allow us to directly specify the transfer functions of the relevant motor systems. Whether gaze stabilization or flight control are considered, the behavioural outputs have to be interpreted as pathway transfer functions which reflect both the properties of the sensor systems in series with the properties of the respective motor system. When deriving transfer functions for the motion vision and the haltere pathways from behavioural data in an earlier study (O28) we were able to avoid the problem of not having the full specifications of the neck motor system by considering ratios of both pathway transfer functions to cancel out neck motor system contributions.

An alternative approach would be to derive the dynamic properties of the neck and flight motor systems in a more direct way by characterizing their functional anatomical organization. To this end we have engaged on studies using x-ray based techniques such as micro-Computer Tomography (μ-CT) to obtain 3-dimensional reconstructions of fly motor systems (O45, A53). The results obtained so far in the course of collaborations with the Natural History Museum London proofed successful in that we were able to achieve sufficient tissue contrast and spatial resolution to digitize and visualizes parts of both the neck and the flight motor system. Based on these data the next step will be to create 3-dimensional models of the motor systems by means of rapid prototyping. Once such models are available we should be in the position to reconstruct pulling planes of direct and indirect muscles which are involved in the actuation of head movement and the control of the flight motor. Figure 7 illustrates the level of resolution achievable with static μ-CT methodology.

Over the last two years, we have accumulated a substantial data base which not only provides valuable information for a reconstruction of the neck and flight motor system but also to quantify other anatomical and brain structures including the volumes of the optic lobes in male and female *Calliphora* (A48).

Another exceptionally interesting aspect of a 3-dimensional anatomical representation based on μ-CT is based on identifying homolog structures across different dipteran fly species. Once those structures have been identified in a sufficient number of animals, principle component analysis enables us to extract those parameters which best describe the anatomical differences between species. For instance, robberflies and blowflies show significant differences regarding the angular range within which the animals are able to move their head relative to the body. They also show marked

differences with respect to the size and power of their flight motor where robberflies are capable of taking on payload (prey) significantly higher than their own body weight. Knowing the principle components associated with interspecific anatomical differences of the flight motor would allow us to correlate them with entirely independent properties or features such as the number of lobula plate tangential cells, flight envelop, or observed modes of motion. Such analysis would offer an incredibly powerful tool to study the evolution of species-specific adaptations in senorimotor ecology – which arguable is one of the keys to understanding general principles of the relationship between sensing and actuation in flying insects.

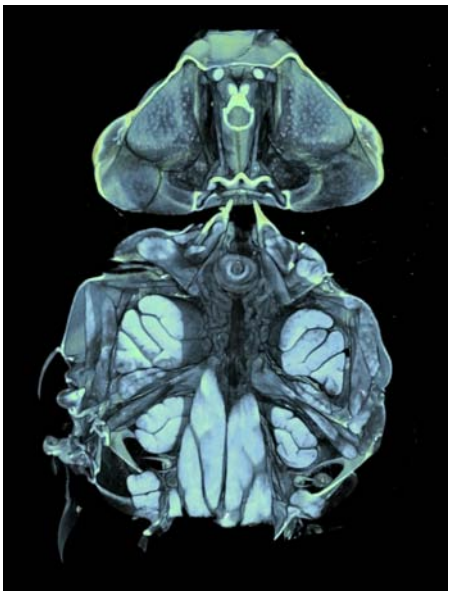

Figure 7: Micro-CT image of the head and parts of the thorax of Calliphora, ventral view. The figure shows a horizontal section through the 3-dimensional structure of the animal's head and thorax which allows us to choose the image plane as required for the rendering of any arbitrary perspective on various anatomical details. Bright and dark structures in the thorax (lower part) and in the neck region represent muscles and cuticle, respectively. The spatial resolution is in the range of 5 μm. In the neck motor region, a pair of direct muscles and their attachment points at specialized cuticular structures, condyles, are visible. In the thorax the dorsoventral (cross-section) and parts of the dorsal longitudinal (partial horizontal section) power muscles can be seen. (work in progress, O45).

Although μ -CT data provide essential 3-dimensional data of functional anatomy, because the data are obtained in dead specimens, inferences about the dynamic properties of the motor systems are difficult to make. To overcome these limitations we are now including more powerful x-ray-based techniques, i.e. *in vivo* synchrotron measurements. We were awarded measuring time for two projects conducted at the Swiss Light Source on the TOMCAT beam line at the Paul Scherre Institute (PSI) to perform ultra fast μ-CT scans in tethered flying flies. The experiments and the analysis of the data is a joint effort of Dr Graham Taylor's group, University of Oxford, the local scientists at the PSI and my group (PI). Our first results are fascinating in that they allow us (a) to segment different tissue types based on phase contrast rather than on issue absorption (b) render different aspects of steering muscle activity related to the control of the fly's wing beat, (c) to quantify volume and length changes of fly power, steering, and neck muscles, (d) to quantify non-linear cuticular deformations which may contribute to efficient lift production due to energy storage in the cuticle, and finally (e) the periodic volume changes of the tracheal system that provides the oxygen supply to the power muscles (A52).

Figure 8 shows a pseudo 3-dimensional image from one of our 4-dimensional data sets, where different anatomical structures are marked by different colour shades. The availability of data regarding the static anatomical organization of motor systems in combination with dynamic synchrotron measurements will be instrumental for a

meaningful reconstruction of the biomechanics involved in flight and gaze stabilization. Also, the 3-dimensional representation of the neck motor system will be instrumental in guiding the placement of electrodes used for electrical stimulation of direct neck muscles in the context of a DSTL-funded PhD project on the dynamics of the neck-motor system.

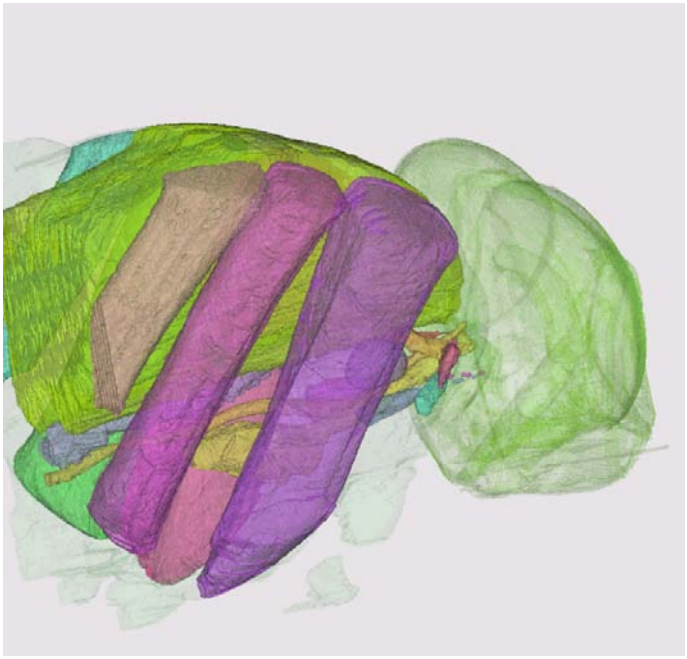

Figure 8: Segmented and colour-labelled anatomical structures obtained from a 4-dimensional data set on Calliphora. Lateral view of the thorax (left) – featuring the prominent dorso-ventral (pink, violet) and dorsal longitudinal (green) muscles of the flight motor – and the head (right) which are connected by the neck motor system. Note that the effective spatial resolution is sufficiently high enough to retrieve the articulations and muscles in both the neck and in the flight motor system. (Schwyn et al. – work in progress).

There are currently strong joint activities between Graham Taylor's and my group to optimize segmentation and rendering procedures of 4-dimensional data sets based on commercially available software packages. Ideally, we would engage on collaborations with companies providing CT scanners and associated software solutions to advance the capability of existing products. 4-dimensional data sets – in particular when obtained from comparatively small insects – still present a significant challenge for tissue segmentation.

Nevertheless, I should expect that due to our integrated approach to understand the control design of the neck motor system we should be able to propose a comprehensive model of an image stabilization system that is truly bio-inspired within the next 3 years.

2.3. ***Neural mechanisms*** underlying multisensory motor control in dipteran flies

Behavioural studies are key to assess the performance limits of a system under study in terms of gaze and flight control. The resulting qualitative and quantitative descriptions guide our studies on the neural mechanisms enabling stabilization reflexes. Together with our data on functional anatomy, the behavioural results provide a framework that constrains the way in which the nervous system may achieve tasks related to motor control.

One of the major challenges the nervous system masters is the transformation of signals obtained in local sensory coordinate into signals that can be used to control movements in coordinate systems essentially defined by the pulling planes of muscles. Regarding the motion vision pathway in dipteran flies – the blowfly *Calliphora* has been particularly well studied in terms of neuronal mechanisms (O33). In the motion vision pathway, noisy local signals indicating retinal motion along the hexagonal ommatidial lattice of the eye are selectively integrated at the lobula plate tangential cells (LPTCs, rev.: O24). Formally, this selective integration of local motion signals in retinal coordinates results in LPTC outputs signalling specific self-motion parameters such as rotation and translation components by processing optic flow information (loc. cit, O1, O3, O33). LPTCs are connected directly and indirectly – via descending neurons – to the neck and flight motor systems. In terms of their preferred self-motion components it has been proposed that LPTCs specifically sense optic flow fields that are induced by the natural modes of motion of a flying insect which are related to the animal's aerodynamic properties (O24, R4).

Such a modal coordinate system set up by the LPTCs would serve as the frame of reference regarding the species-specific sensorimotor transformations. Information obtained from other sensors indicating state changes, for instance the ocelli, could then be used to speed up the response within the inherently slow motion vision pathway (O34, see above). This way the spatial resolution required to sense specific modes of motion is established by choosing and integrating those local directional inputs which match the optic flow vectors generated during a particular mode of motion. As the compound eye in flying insects have an enormous number – several hundreds in *Drosophila*, several thousands in *Calliphora* – the pool of local inputs to choose from potentially allows flying insects to very precisely set up a modal coordinate system in the motion vision pathway that satisfies its aerodynamic control requirements. The ocelli, on the other hand, provide only very crude spatial information about any state changes, but are way faster than the motion vision pathway (O20, O34, O28, 29).

The overall performance of stabilization reflexes is even further increased regarding the bandwidth the systems are able to cope with, by including fast mechanosensory signals, for instance, from the halteres (rev.: O24). As we know from both behavioural studies (O37, rev.: O24) and electrophysiology (O30) the halters contribute to gaze and flight stabilization. Recent work indicates, though, that for gaze stabilization halter signals are used in a feed forward way to reduce retinal slip speeds into a dynamic range the motion vision pathway can operate in (O37, O41). For flight control, however, the signals from the halteres provide immediate negative feedback to the flight motor (Elzinga et al. 2011).

One of the major efforts in my lab concerns the characterization of response properties in optic flow processing LPTCs. This is because:

- LPTCs assume a significant role in the sensorimotor transformation. Any non-linear processes along the pathway involving motion vision may only be identified in terms of neuronal activity measurements but not necessary at the behavioural level.

- The response properties of some LPTCs directly reflect multisensory integration as they are electrically connected to descending neurons which also receive input from other modalities.
- The specific receptive field organization of LPTCs allows us to derive the self-motion components different species of flying insects have evolved to detect and most likely to control.
- LPTCs are an ideal stage in the sensorimotor pathway to investigate state-dependent visual information processing. This topic is of major interest when power consumption becomes in issue due to limitation in payload on small terrestrial and aerial autonomous systems.
- LPTCs also are likely to be a key stage regarding the integration of inner-loop stabilization reflexes and outer-loop tasks related to navigation and distance as well as proximity estimation.

LED-based stimulation device to map the receptive field of optic flow processing interneurons (LPTCs) in flying insects.

In previous years we used fast CRT displays to determine general visual response properties of LPTCs and neck motor neurons (e.g. O31, O36, O26, O30). To assess the distribution local preferred directions and motion sensitivities within the receptive field of LPTCs we mainly applied a dedicated electro-mechanical stimulation device optimized to speed up experimental protocols (O2). To gain more flexibility in terms of visual stimulation we recently re-designed the original stimulation device by replacing the mechanical stimulus, a black disk moving on a circular path, with LED displays. Figure 9 shows the completed device.

Figure 9: The re-designed stimulation device consist of a meridian metal frame equipped with 6 LED panels mounted at +- 75, 45 and 15 degrees elevation. The spacing of the LEDs and the rate at which their luminance values are refreshed are adapted to the properties of the visual system under moderate light levels. The fly in positioned in the centre of the meridian frame which can be moved around the animal to cover an overall azimuthal range of about 315 degrees. Positioning of the recording electrode is achieved by a 3 DoF electronic micro-manipulator under visual magnification using a stereo microscope. (photograph: Ben Hardcastle).

The device is controlled by a lab-view interface and allows us to deliver visual motion stimuli to determine both the local directional tuning of LPTCs and their dynamic response properties. It has been successfully tested in experiments on blowflies so far, but will also be instrumental to map the receptive fields of other dipteran flies such as robberflies, horseflies and hoverflies.

Receptive field organization of optic flow processing interneurons in various dipteran fly species.

Current research in collaboration with Dr Graham Taylor, Oxford, and Dr Sean Humbert, UMD, has made considerable progress in support of the mode sensing hypothesis (e.g. R4). Free flight experiments in Sean Humbert's lab have successfully been carried out to quantify the modes of motion in *Calliphora*. We are currently working on a scientific publication that relates the modes of motion to the directional templates of blowfly LPTCs to establish the relationship between sensory and motor control coordinate systems (O44). This work benefits from a joint AFOSR research grant to Sean Humbert and myself, where we focus on the interactions between the motion vision pathway and the ocelli (see above) and will be reported in detail in a separate paper.

To gain further support for the mode sensing hypothesis and to facilitate the translation of biological control design principles into enabling technology we have applied for additional funding with AFOSR (decision pending). In order to show that the mode sensing hypothesis has general implication for biological control we will have to apply a comparative approach. Across several dipteran flies, orthopterans, and potentially Lepidoptera we will characterize the receptive fields of optic flow processing interneurons and the animals' flight dynamics. These species cover a sufficiently broad spectrum of flight behaviours/aerodynamic properties to test whether the alignment of sensory and motor coordinate systems is a general principle amongst flying insects.

In my lab we have started recording from optic flow processing interneurons in robberflies, horseflies and hoverflies. Several singular recordings from US robberfly species such as *Laphria* and *Diogmites* – caught by/or in collaboration with Ric Wehling, AFRL, Eglin – have shown that spiking LPTC in robberflies have response properties similar to those found in the blowfly. Although we have not yet performed intracellular recordings required for individual identification, the physiological results so far suggest new world robberflies to employ H1-, V1-, and V2-like cells sensitive to yaw, combined pitch/roll and roll, respectively. I presented some of those results in earlier reports.

As the provision with new world robberfies for experiments in the UK turned out to be difficult we have now identified a species common at the English south coast, *Dysmachus trigonus* (Fig 6), which appears from early May until end of August. One of my postdocs, Dr Kit Londgen, was funded on this AFRL grant and is currently funded by the joint AFOSR grant between Sean Humbert and I, has succeeded to perform extracellular recordings from *Dysmachus*, which is slightly smaller in size than *Calliphora*. He obtained the first LPTC receptive field maps from this robberfly species and also data on the temporal response properties of these cells. What Kit also

found in the lobula plate of *Dysmachus* is a class of directional selective cells which possess comparatively small receptive fields located slightly below the eye equator in the frontal to frontolateral visual field. Cells with such response properties are not frequently encountered during extracellular recordings from *Calliphora*, even though behavioural experiments on the elevation sensitivity of compensatory head roll movements suggest a neural mechanism that specifically enhances the response to visual motion just below the external horizon (see below).

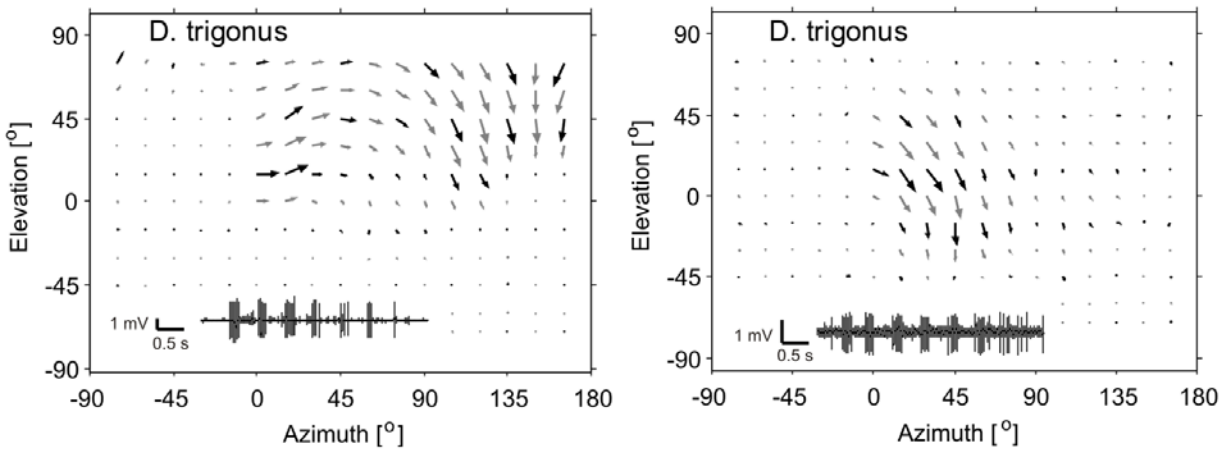

Figure 10: Receptive field organization of spiking lobula plate tangential cells in Dysmachus trigonus. Left: The local preferred directions in the receptive field of this cell depend on the azimuth and the elevation where the directional tuning is assessed. The pattern looks similar to that observed in a blowfly dCH cell (O10) – although the dCH cell in blowflies does not generate any action potentials. Right: The distribution of local preferred directions has similarities to that of a blowfly V1 receptive field (O10) – here, however, the receptive field seems to be more confined to the frontolateral region of the visual field. Insets in both panels show the spiking response over time to a number of consecutive motion stimulus cycles. Note the strongly structured response where phases of high spike rates (during movement in the preferred direction) are followed by inhibition (during movement in the null direction) which indicates that the cell receives input from fully opponent elementary movement detectors (e.g. rev.: O24).

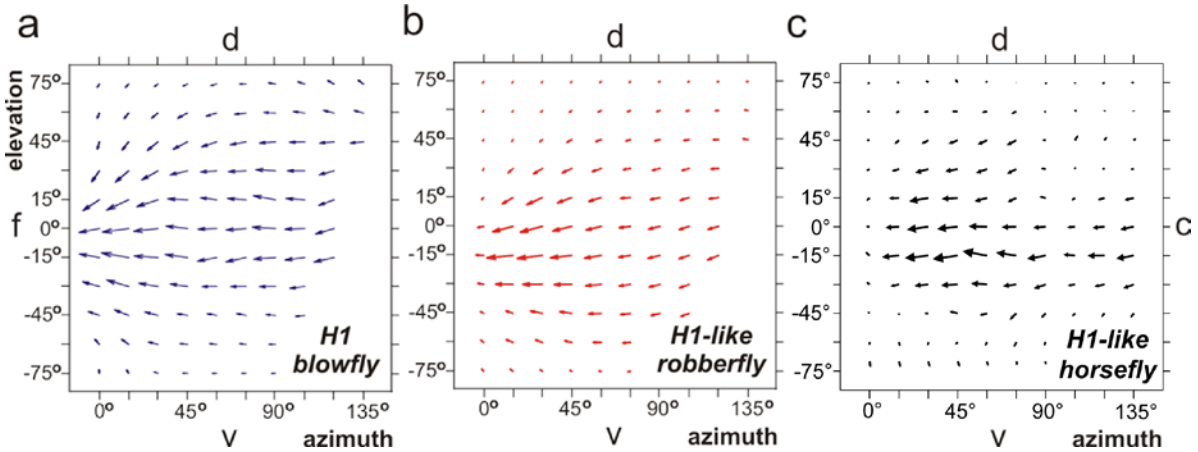

Figure 11: Partial receptive fields of (a) the H1-cell in the blowfly Calliphora, (b) an H1-like cell in the robberfly Laphria, and (c) an H1-like cell in the horsefly Hematopota. The H1-cell is sensitive to yaw-rotations while being inhibited during forwards translation. This cell was found in all dipteran flies studied so far.

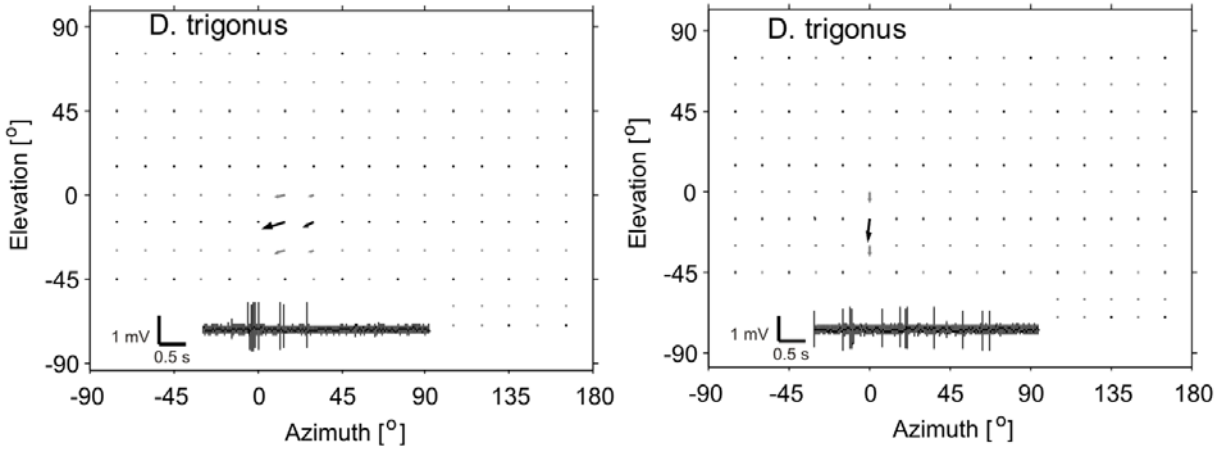

Figure 12: Small-field directional selective cells in the lobula plate of Dysmachus. These cells show an extremely confined receptive field of no more than 20-30 degrees in diameter located just below the eye equator in the frontal visual field. It is unlikely that the localized response of these cells is the consequence of a highly nonlinear integration process which requires simultaneous inputs from many direction selective elements before a spike may be generated while local motion stimuli only result in subthreshold membrane potential changes. The cell sensitive to vertical downward motion (right) could potentially contribute to a neural mechanism that stabilizes the position of the external horizon just below the animal's eye equator. For further explanation, see text.

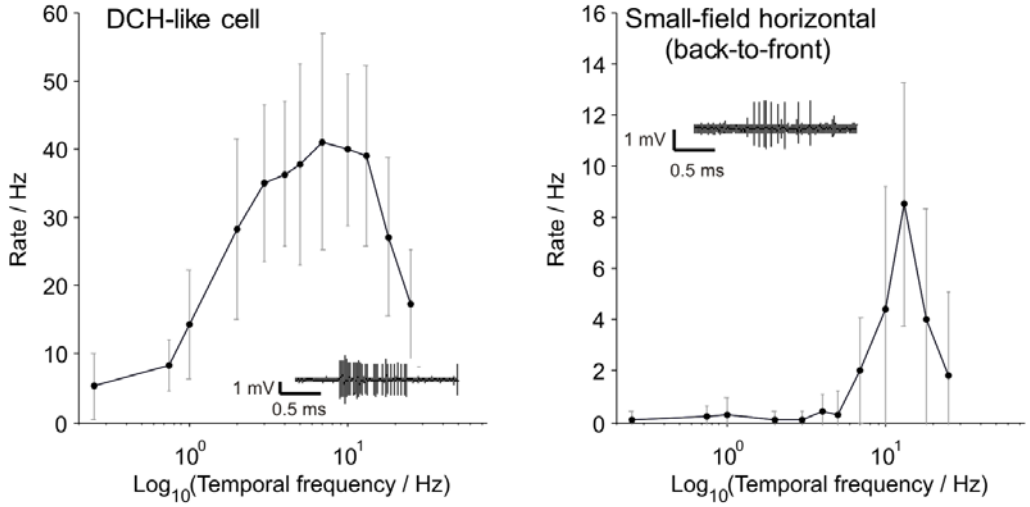

Figure 13: Temporal frequency tuning of wide-field and small-field LPTCs in Dysmachus. Moving a visual grating with a fixed spatial wavelength at different velocities shows that small-field cells possess a significantly narrower temporal frequency tuning than wide-field cells. Together with the marked difference in receptive field size (Fig 11), this suggests small-field cells may be involved in small target detection as opposed to the estimation of self-motion.

The conclusions of our studies on robberfly LPTCs so far are: (i) Spiking wide-field LPTCs in robberflies most likely serve a similar function like blowfly wide-field LPTCs do – i.e. the estimation of self-motion parameters and (ii) small-field LPTCs may either be adapted to detect small targets or may be involved in horizon detection in case they have vertical motion preferences. The former function, small target

detection, may be similar to that of figure detection cells (FD-cells, Egelhaaf 1985) in the blowfly. Further experiments will be required to study their response properties in more detail. An alternative interpretation, at least for cells sensitive to vertical motion, would be that they support a horizon detection mechanism reported in the context of gaze stabilization in blowflies (see above). Hengstenberg proposed such mechanism based on earlier work on gaze stabilization which was further substantiated by an increased gain of compensatory head roll just below the eye equator (Fig 14, A6). This increased gain could not be explained by the receptive field organization of the VS-cells, a subset of wide-field LPTCs indicating rotations around the fly's horizontal body axes (O1, O3). Although small-field LPTCs similar to those encountered in the robberfly have not been reported in blowflies, some blowfly neck motor neurons show receptive field with similarly small receptive fields (O26).

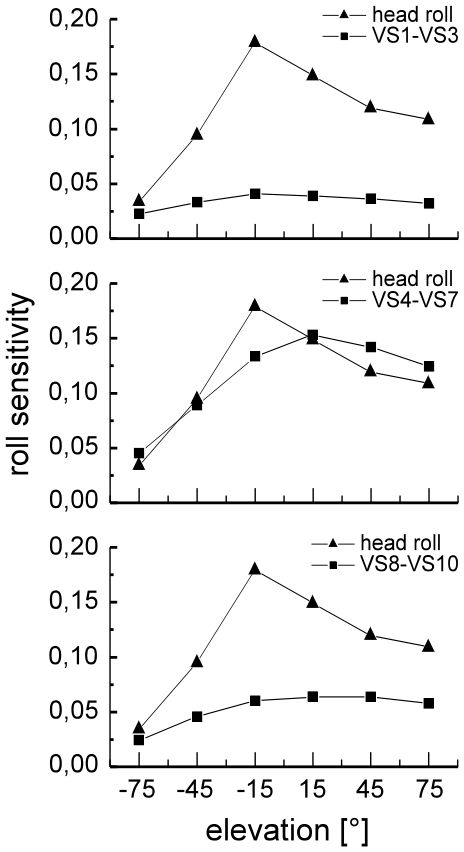

Figure 14: Gain of compensatory head roll (filled triangles) and quantitatively estimated contributions of groups of VS cells (filled squares) in Calliphora. The head roll sensitivity was determined by oscillating a narrow horizontal bar covering 90 degree in azimuth of the lateral visual field at 0.63 Hz and at an amplitude of +/- 15 degrees. The resulting response gain is plotted as a function of elevation (all three panels). The same stimulus was projected into the receptive fields of three groups of VS-cell to estimate the neurons' responses. Although the combined and normalized response estimate of VS4-VS7 closely follows head roll sensitivity, at an elevation of -15 degree there is a significant difference between the behavioural data and the estimated neural responses (middle panel). This result suggests an additional neural mechanism contributing to head roll sensitivity just below the eye equator. (Data from A6.)

State-dependent processing of optic flow.

Information processing in the nervous system is a significant cost factor in the overall metabolic energy budget of an animal. Sensory cells in particular may consume a considerable amount of energy in an attempt to reduce response delays at the expense of low input resistances and high ion currents across the cell membrane. The same is true for large integrating cells such as the LPTCs. These cells have a comparatively low input resistance resulting in a resting potential of only around -50 mV compared to -70 mV in other nerve cells. The low input resistance reduces the membrane time constant and speeds up the neurons' responses. On the other hand a low input

resistance due to many open ion channels requires more energy to maintain the required concentration gradients of ion species involved in signalling such as sodium, potassium, calcium and chloride. To a certain degree this is a necessary investment as it enables short response delays to visual stimulation. At the sensory and central processing levels this results is a trade-off between higher bandwidth and higher energy consumption (Niven and Laughlin 2008).

Such trade-off concerns not only the immediate costs of information transfer in the nervous system. The consequences of inaccurate sensory information processing may be by far more severe. Erroneous sensory signals may result in massive waist of metabolic energy due to imprecise flight manoeuvres executed by the power muscles of the flight motor, which arguably consumes even more energy than the nervous system. Altogether, the most appropriate strategy would be to safe energy when the animal faces a limited dynamic stimulus range and to invest more energy only when the stimulus dynamics increase – which normally is the case when the animal performs any kind of locomotor activity.

Two years ago Kit Longden applied an octopamine agonist chlordimephorm (CDM) – a drug known to push the nervous system of insects into a fictive locomotor state – to the blowfly haemolymph while recording from spiking LPTCs. The immediate effect was that the cells increased their spontaneous spike rate, responded faster to visual stimuli and transmitted more information about directional motion (O31). He continued his work to publish another paper where he also studied the impact of CDM on the temporal response characteristics of LPTCs (O36). Several other labs also started working on the relationship between locomotor state and visual processing which has now become an established research area in insect motion vision. We also published a dispatch in *Current Biology* featuring work on this topic (O39). In the following I will present some of the more recent results Kit presented in a dedicated symposium on state-dependent information processing at the International Society of Neuroethology in Maryland, USA. Finally, I will summarize the findings and will discuss the relevance of the work for the design of micro air vehicles.

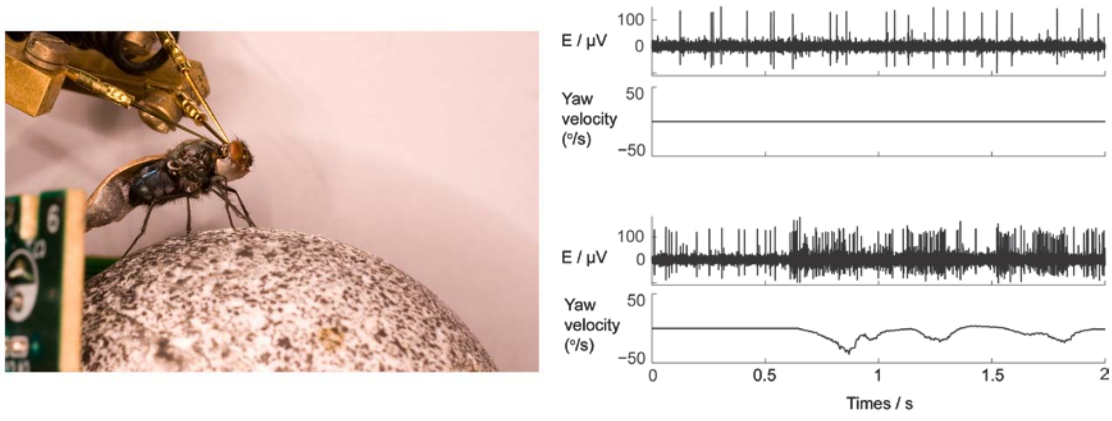

Figure 15: Simultaneously monitoring neural activity and walking in tethered blowflies. Left: A blowfly is walking on an air-suspended styrofoam ball the rotations of which are measured with photoelectric devices (optical mice) and converted into a yaw signal. At the same time the spiking activity of the H2-cell is recorded using tungsten electrodes. Right: The upper panel shows spiking activity (1st trace) when the fly is at rest as indicated by the zero yaw velocity (2nd trace). The lower panel shows increased spiking activity (1st trace) when the fly spontaneously starts to move (2nd trace). (Longden, work in progress).

Rather than staying with the drug CDM, Kit has now set up an experimental rig which allows him to monitor the walking behaviour of *Calliphora* while recording the neural activity of spiking LPTCs (Figs. 15, 16). He also applied octopamine, the neuro-modulator involved in changing the neuronal activity and switching the animal's metabolic pathways in preparation for flight. Additionally, he used an octopamine antagonist in an attempt to reduce the effect walking has on processing visual motion in LPTCs (Fig. 17).

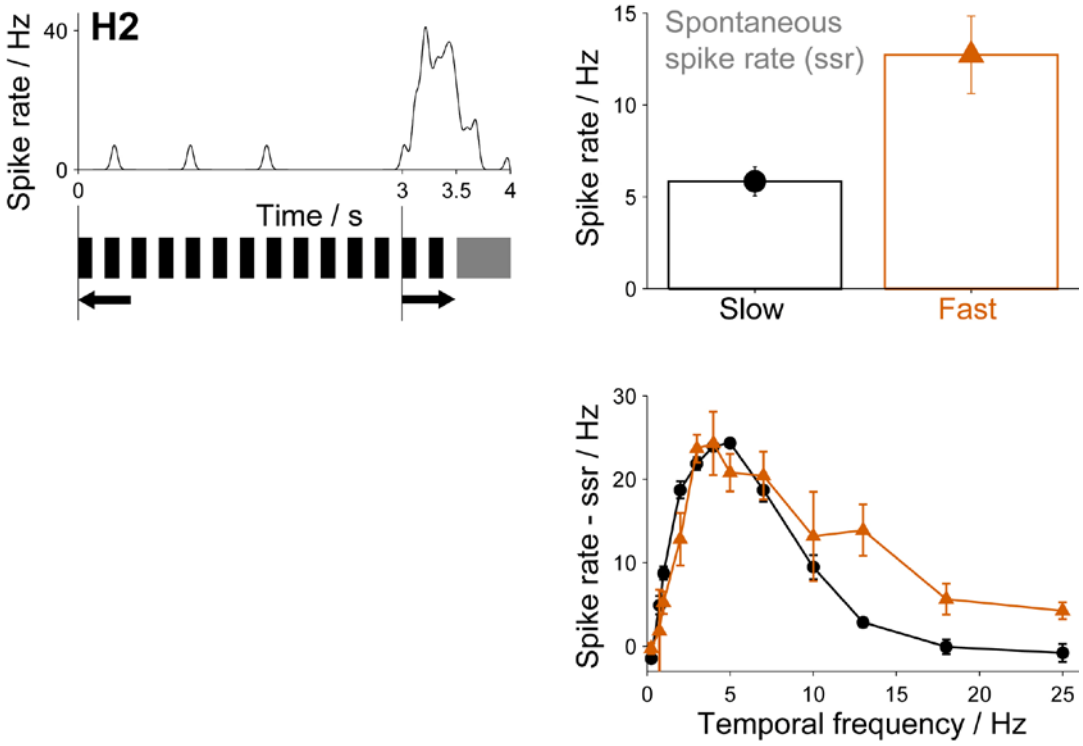

Figure 16: Using the setup shown in the previous figure, the fly is presented with visual stimuli which include two different components. Upper left panel: A visual grating is first moved in the anti-preferred direction of a recorded H2-cell. This stimulus inhibits spiking in the cell. Immediately after 3 s of anti-preferred direction movement, the stimulus is moved into the cell's preferred direction for 500 ms, followed by the presentation of a blank screen of average brightness. The response, convolved with a Gaussian filter, is shown on top of the stimulus trace. Upper right panel: The spontaneous spike rate (ssr) – i.e. without the motion stimulus – is also recorded and categorized according to a threshold criterion related to the current walking speed of the animal which is either slow or fast. The ssr in fast walking animals is significantly higher than in slowly walking animal. Lower right panel: The temporal frequency tuning of the H2-cell. The response minus ssr is plotted against different temporal frequencies in slowly (black) and fast (orange) walking flies. At high temporal frequencies fast moving flies show a stronger response than slowly moving flies which suggests that walking increases the bandwidth of the cell due to reduced motion adaptation. (Longden, work in progress).

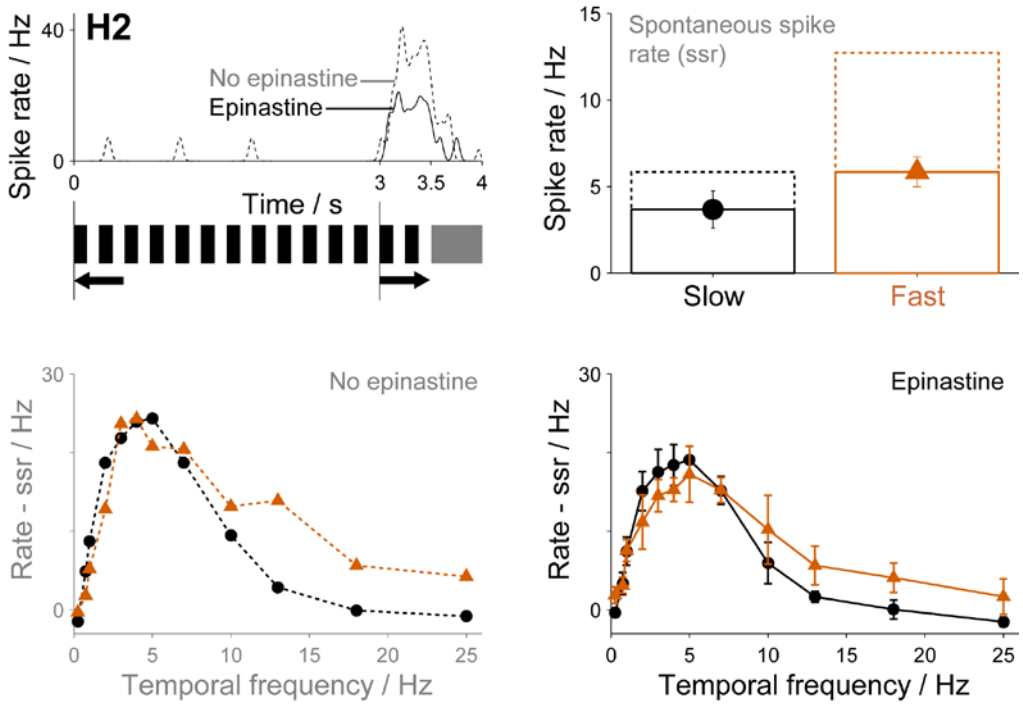

Figure 17: The same protocol as described in figure legend 16, applied to two different experimental conditions. Solid curves indicate results obtained under the influence of epinastine, an octopamine antagonist. Dotted curves were obtained without epinastine (controls). Black and read curves give data gathered during slow and fast walking, respectively. While epinastine reduces the impact of walking on the ssr (upper right panel), its effect on the temporal tuning curve is comparatively small. Octopamine, thus, seems to be involved in increasing the ssr and has a small effect on the cell's changes in temporal frequency tuning during walking (lower right panel). (Longden, work in progress).

Our results over the last 2 years support the following conclusions regarding the mechanisms in place to produce state-dependent changes in visual motion processing:

- CDM increases the spontaneous activity (ssr), reduces the response delay, and increases the dynamic output range of the cell by an enhanced negative signalling range.
- Locomotion on its own increases the spontaneous activity (ssr) significantly, has no direct effect on the temporal frequency tuning but affects motion adaptation which increases the sensitivity to higher temporal frequencies.
- Locomotion in combination with motion adaptation reduces the response delay and increases the gain for all temporal frequencies in a physiological time window of 20-80 ms after stimulus presentation.
- Octopamine antagonist reduces both the ssr and the response gain, and increases the response delay.

Altogether the effects suggest that blowflies save energy during rest by lowering the spontaneous spike rate and response gain to visual motion. Only when switching to an active locomotor state the response delays are reduced and the bandwidth of the cells is increased. Although octopamine is involved in state-dependent motion processing the effects may be mediated through other mechanisms, for instance motion adaptation. Any impact on the temporal frequency tuning of the cell, therefore, may

be due to neuro-modulator action in combination with an expanded stimulus/velocity distribution during locomotion.

The significance of the neural mechanisms underlying state-dependent visual motion processing is obvious from the design perspective regarding the development of autonomous micro air vehicles. Size and payload limitations do not permit the use of power-hungry high throughput floating point devices for the processing and integration of sensor signals including their transformation into actuator commands. This is where, firstly, task-specific integration of local motion information becomes particularly efficient which results in an output signal that can be applied immediately to control state changes. And secondly – assuming analogue processing devices in VLSI technology – where continuous adjustments of input and output bandwidth may mitigate the problems of power consumption in two ways: (i) Saving energy when the input bandwidth is low and (ii) implementing circuits in low-power VLSI in the first place.

Fly-robot interface for studying multisensory integration.

This ongoing work aims to establish a closed-loop platform that allows us to record the activity of a spiking LPTC, the H1-cell, in a fly that is mounted on a two-wheeled robot. The recorded spiking activity is converted into a command signal applied to the motors driving the robot wheels so that the fly does not collide with any obstacles. A simplified version of such a closed-loop system has been fully characterized and used to assess the performance of the H1-cell as a motion vision sensor under different feedback control laws in an image stabilization task (O38, C4, C5).

The dynamics of the robot are chosen so that several sensory systems will be stimulated, including the antennae, halteres and compound eyes. By systematically disabling individual sensor systems we will test whether sensory modalities other than motion vision impact on the activity of the H1-cell and other spiking LPTCs while the robot is moving under closed-loop conditions. From previous open-loop studies we already know that the V1-cell, for instance, reflects the activity of other sensory systems, e.g. the ocelli. One of the challenges of this project has been to miniaturize electrophysiological equipment so it does not add to much inertia to the closed-loop robotic platform while still enabling stable extracellular recordings. After we have now succeeded to design a miniaturized and stable recording module we will soon be able to perform the first experiments with the fly steering the robot.

Related to this project is our attempt to develop a miniaturized extracellular amplifier small enough to fit into the head capsule of a blowfly – a project funded by the HFSP trust. The amplifier has already been successfully produced and tested (C3). We are still working on electrode chip that provides the front end to the systems. It will consist of 3 differential recording channels to measure the signals in spiking LPTCs in freely or semi-freely moving flies the trajectory of which will be monitored by high speed video cameras. The video footage will be used to reconstruct the fly's self-motion components which can then be correlated with the neural activity.

In both these projects we should also be able to retrieve any traces of efference copies (forward models) the fly might be using to improve its sensoimotor control performance.

2.4. ***Modelling*** of multisensory motor control design

If the performance of a control system is readily captured by a set of transfer functions which are normally sufficient to specify control architectures, why do we bother about (a) neuronal mechanisms and (b) mechanistic or biomechanical models? Why should we not just go ahead and implement on an MAV the system properties described in terms of phenomenological models?

There are a couple of answers to this question which are often neglected when it comes to implementation. One of the major points is that the nervous system in insects with its comparatively limited capacity in terms of number of neurons has to serve several high specification control tasks simultaneously. Although the life of an insect is concerned more or less only with two tasks – feeding and mating – the enabling motor programmes are quite diverse as they do not simply produce one fixed behavioural sequence but rather accomplish the tasks in a context-dependent way. Foraging flights, where navigating to a rewarding feeder is the primary objective, may be interrupted by collision avoidance manoeuvres or external disturbances due to gusts of wind which need to be compensated for to maintain aerodynamic stability. Often this means that incoming sensory information has to be processed and fed back into the flight controller in very different ways using one and the same final neuronal pathway to the motor systems. Another factor that has been pointed out recently is the limited amount of energy available to the insect for both powering up the muscles and providing the nervous system (see above). And finally, the way in which insects acquire information and convert sensor readings into actuator commands depends on the structural and dynamic properties of the sensors and the functional organization as well as the dynamics of the motor systems they control. This is probably true in robotics, too, only that the task space of most robots is comparatively well specified which often allows for a simpler mechanical and control design. Insects use the same hardware to solve very different tasks and need to modulate their sensorimotor transformation depending on which task is currently being controlled. Switching, for instance, between olfactory-driven navigation and collision avoidance, may be required within a fraction of a second.

The integration of inner-loop reflex behaviour and outer-loop voluntary – or task related – behaviour imposes a fundamental constraint on the way in which different modelling approaches may be exploited. So far we applied mostly linear systems approaches to work out the way in which various sensory modalities are combined in fly gaze stabilization (see above, O37, O41). In collaboration with Dr Reiko Tanaka, Bioengineering, Imperial College, we develop a closed-loop simulation platform that emulates gaze stabilization in a linear control engineering framework including systems identification methods. But it became obvious already that several experimental results are not easily explained by the linear combination of transfer functions (see above – compound eye/ocellar interactions). We therefore combine different approaches always starting with the most parsimonious model, i.e. a linear one. In cases where we do not capture the overall behaviour of the system we add

complexity by including static nonlinearity to mechanistic models (see above). Finally, as mentioned earlier, biomechanical models will augment our modelling efforts in particular when it comes to the connection between sensing and actuation where, in biology, much of the computational workload is reduced by the choice of the mechanical design and material properties.

Biomechanical and mechanistic neuronal modelling will be important to identify those physiological mechanisms which make biological systems special in terms of their performance. As mentioned earlier – the most interesting question is as to how different non-linear systems manage to produce a system's output that looks by and large linear. In biology, non-linearities may as well be beneficial, despite all the risks they bear from the perspective of a control engineer.

3. Conclusion:

Besides the academic outputs produced during the period of funding – and probably beyond – one of the most important outcomes over the last couple of year has been a clear research agenda for my lab. While collaborating with the groups of Graham Taylor and Sean Humbert my research has shaped into a system neuroscience approach that combines quantitative behaviour, electrophysiology, functional anatomy and modelling to advance our understanding of biological control design – with a strong emphasis on the underlying neuronal mechanisms. In particular the interactions with Sean Humbert have resulted in several tangible outputs, e.g. the proof of concept study showing that LPTC receptive fields can be successfully used to control orientation, proximity and forward speed of a quadropter (O35) or the development of an ocellar senor (C6). Future interactions between my group and the groups of my collaborators will aim to further discover and exploit biological design principles in the context of control and navigation of autonomous robotic systems. The emphasis will be to advance autonomy and manoeuvrability by multisensor fusion, dynamic range fractioning and the integration of inner- and outer loop control.

Holger G Krapp London, 13. August 2012

4. Additional References:

Egelhaaf, M. (1985) On the Neuronal Basis of Figure-Ground Discrimination by Relative Motion in the Visual-System of the Fly. 2. Figure-Detection Cells, A New Class of Visual Interneurones. *Biol. Cybern.* **52**:195–209.

Elzinga M. J., Dickson W.B., and Dickinson M.H. (2011) The influence of sensory delay on the yaw dynamics of a flapping insect. *H. R. Soc. Interface*, doi:10.1098/rsif.2011.0699.

Gilbert C., Gronenberg W., Strausfeld N.J. (1995) Oculomotor control in Calliphorid flies: Head movements during activation and inhibitions of neck motor neurons corroborate neuroanatomical predictions. *J. Comp. Neurol.* **361**:285-297.

Haag J., Wertz A., and Borst A. (2007). Integration of lobula plate output signals by DNOVS1, an identified premotor descending neuron. *J. Neurosci.* **27**:1992-2000.

Hausen K. (1993) Decoding retinal image flow in insects. *Rev. Oculomot. Res.* **5**:203-235.

Hengstenberg, R. (1993). Multisensory control in insect oculomotor systems. *Rev. Oculomot. Res.* **5**:285-98.

Niven J. E. and Laughlin S.B. (2008) Energy limitation as a selective pressure on the evolution of sensory systems. *J. Exp. Biol.* 211, 1792-1804.

Rosner R., Egelhaaf M., Grewe J., and Warzecha A.K. (2009) Variability of blowfly head optomotor responses. *J. Exp. Biol.* 212, 1170-1184.

Strausfeld N.J., Seyan H.S., Milde J.J. (1987) The neck motor system of the fly *Calliphora erythrocephala*. *J. Comp. Physiol. A* **160**:205-224.

5. List of Publications:

Diploma Thesis:

Krapp H.: Ein Verfahren zur schnellen Bestimmung der lokalen Vorzugsrichtung und Bewegungsempfindlichkeit im rezeptiven Feld von visuellen Interneuronen der Schmeißfliege *Calliphora erythrocephala*. Diplomarbeit. Eberhard-Karls-Universität Tübingen 1992.

PhD Thesis:

Krapp H.: Repräsentation von Eigenbewegungen der Schmeißfliege *Calliphora erythrocephala* in VS-Neuronen des dritten visuellen Neuropils. Dissertation, Eberhard-Karls-Universität, Tübingen, 1995.

Publications in refereed journals:

O1. **Krapp H.G.** and Hengstenberg R.: Estimation of self-motion by optic flow processing in single visual interneurons. *Nature*, **384**: 463-466, (1996)

O2. **Krapp H.G.** and Hengstenberg R.: A fast stimulus procedure for determining local receptive-field properties of motion-sensitive visual interneurons. *Vision Research*, **37**: 225-234, (1997)

O3. **Krapp H.G.**, Hengstenberg B., and Hengstenberg R.: Dendritic structure and receptive field organization of optic flow processing interneurons in the fly. *Journal of Neurophysiology*, **79**: 1902-1917, (1998)

O4. Gabbiani F., **Krapp H.G.,** and Laurent G.: Computation of object approach by a wide-field, motion- sensitve neuron. *Journal of Neuroscience*, **19**: 1122-1141, (1999)

O5. Gabbiani F, Laurent G, Hatsopoulos N, and **Krapp H.G.**: The many ways of building collision-sensitive neurons. *TINS*: **22**, 437-438, (1999)

O6. **Krapp H.G.** Neuronal matched filters for optic flow processing in flying insects. *International Review of Neurobiology*, **44**: 93-120, (2000).

O7. Franz M.O. and **Krapp H.G.**: Wide-field, motion-sensitive neurons and optimal matched filters for optic flow. *Biological Cybernetics*, **83**: 185-197, (2000).

O8. Petrowitz R., Dahmen H., Egelhaaf M., and **Krapp H.G.**: Arrangement of optical axes and the spatial resolution in the compound eye of the female blowfly. *Journal of Comparative Physiology A*: **186**: 737-746, (2000).

O9. Karmeier K., Egelhaaf, M., and **Krapp H.G.**: Early visual experience and the receptive field organization of optic flow processing interneurons in the fly motion pathway. *Visual Neuroscience*, **18**: 1-8, (2001).

O10. **Krapp H.G.**, Hengstenberg R., and Egelhaaf M.: Binocular input organization of optic flow processing interneurons in the fly visual system. *Journal of Neurophysiology*, **85**: 724-734, (2001).

O11. Gabbiani F., **Krapp H.G.**, Koch C., and Laurent G.: Multiplicative computation in a looming sensitive neuron. *Nature*, **420**: 320-324, (2002).

O12. Egelhaaf M., Kern R., **Krapp H.G.**, Kretzberg J., Kurtz R., and Warzecha A-K.: Neuronal encoding of behaviourally relevant visual-motion information in the fly. *TINS*: **25**, 94-100, (2002).

O13. Karmeier K., **Krapp H.G.,** and Egelhaaf M.: Robustness of the tuning of fly visual interneurons to rotatory optic flow. *Journal of Neurophysiology*, **90**: 1626-1634 (2003).

O14. Matheson T., **Krapp H.G.,** and Rogers S.M.: Plasticity in the visual System is correlated with a change in life-style of solitarious and gregarious locusts. *Journal of Neurophysiology*, **91**: 1-12 (2004).

O15. Franz MO, Chahl JS, and **Krapp H.G.:** Insect inspired estimation of self-motion. *Neural Computation* **16**: 2245-2260, (2004).

O16. Gabbiani F, **Krapp H.G.**, Hatsopoulos N., Mo C-H., Koch C. and Laurent G.: Multiplication and stimulus invariance in a looming-sensitive neuron. *Journal of Physiology Paris* **98**, 19-34. (2004).

O17. **Krapp H.G.** and Gabbiani F.: Spatial distribution of inputs and local receptive field properties of a wide-field, looming sensitive neuron. *Journal of Neurophysiology*, **93**: 2240 – 2253, (2005).

O18. Karmeier K., **Krapp H.G.,** and Egelhaaf M: Population coding of self-motion: Applying Baysian inference to estimate the performance of visual interneurons in the fly. *Journal of Neurophysiology*, **94**: 2182 – 2194, (2005).

O19. Gabbiani F. and **Krapp H.G.**: Spike-frequency adaptation and intrinsic response properties of an identified, looming sensitive neuron. *Journal of Neurophysiology*, **96**, 2951-2962, (2006).

O20. Parsons M.M., **Krapp H.G**., and Simon B. Laughlin: A motion sensitive neuron responds to signals from the two visual systems of the blowfly, the compound eyes and the ocelli. *Journal of Experimental Biology*, **209**, 4464 - 4474, (2006).

O21. Peron S., **Krapp H.G.**, and Gabbiani F.: Influence of electrotonic structure and synaptic mapping on the receptive field properties of a collision detection neuron. *Journal of Neurophysiology*, **97**, 159 – 177, (2007).

O22. Rogers S.M., **Krapp H.G.**, Burrows M., and Matheson T.: Compensatory plasticity at an identified pathway tunes a viso-motor pathway. *Journal of Neuroscience*, **27**, 4621 – 4633, (2007).

O23. **Krapp H.G.:** Polarization vision: How insects find their way by watching the sky. *Current Biology*, **17**, R557 - R560 (2007).

O24. Taylor G.M. and **Krapp H.G.**: Sensory systems and flight stability: What do insects measure and why? *Advances in Insect Physiology*, **34**, 231 – 316 (2007).

O25. **Krapp H.G.**: Estimation of self-motion for flight and gaze stabilization. *Navigation*, **55**, 147-158 (2008).

O26. Huston S.J. and **Krapp H.G.**: Visuomotor transformation in the fly gaze stabilization system. *PLoS Biology*, **6**(7):e173 (2008).

O27. Saleem A, **Krapp H.G.**, and Schultz S.R.: Spike-triggered independent component analysis: application to a fly motion-sensitive neuron. *Visual Neuroscience*, **8**(13):2, 1-16 (2008).

O28. **Krapp H.G.**: Sensory Integration: Neuronal adaptations for robust visual self-motion adaptation. *Current Biology*, **19**(10), R413-416 (2009).

O29. **Krapp H.G.**: Ocelli, *Current Biology*, **19**(11), R435-437 (2009).

O30. Huston S.J. and **Krapp H.G.**: Non-linear integration of visual and haltere inputs in fly neck motor neurons, *Journal of Neuroscience*, **29**, 13097-13105 (2009).

O31. Longden K.D. and **Krapp H.G.**: State-dependent receptive field properties of optic flow processing interneurons, *Journal of Neurophysiology*, **102**, 3606-3618 (2009).

O32. Rogers S.M., Harston G., Kilburn-Toppin F., Matheson T., Burrows M., Gabbiani F., and **Krapp H.G.**: Differences in the spatiotemporal receptive field of a looming-sensitive neuron caused by phase change in the Desert Locust. *Journal of Neurophysiology*, **103**, 779-792 (2010).

O33. **Krapp H.G.**: Sensorimotor Transformation: From visual responses to motor commands. *Current Biology*, **20**(5), R236-R239, (2010).

O34. Parsons M.M., **Krapp, H.G.**, and Laughlin S.B.: Sensor fusion in identified visual interneurons. *Current Biology* ,**20**(7), 624-628 (2010).

O35. Hyslop A., **Krapp H.G.**, and Humbert J.S.: A control theoretic interpretation of directional motion preferences in optic flow processing interneurons. *Biological Cybernetic*, **103**(5), 353-364, DOI: 10.1007/s00422-010-0404-8 (2010).

O36. Longden K.D. and **Krapp H.G.**: Octopaminergic modulation of temporal frequency coding in an identified optic flow-processing interneuron. *Frontiers in Systems Neuroscience*. **4**:153. doi: 10.3389/fnsys.2010.00153 (2010)

O37. Schwyn, D., Hernandes Heras F.J., Bolliger, G., **Krapp H.G.**, Tanaka, RI.: Characterization of insect gaze control systems. *18th World Congress of International Federation of Automated Control (IFAC)*, Milan, (2011)

O38. Ejaz N., Peterson K.D., **Krapp H.G.**: An Experimental Platform to Study the Closed-loop Performance of Brain-machine Interfaces. *Journal of Visualized Experiments*, **49**. http://www.jove.com/index/Details.stp?I D=1677, doi: 10.3791/1677 (2011).

O39. Longden K.D. and **Krapp H.G.**: Sensory Neurophysiology: Motion vision during motor action. *Current Biology*, **21**, R650-R652 (2011).

O40. Saleem A.B., Longden K.D., Schwyn D., **Krapp H.G.**, Schultz S.R.: Pattern and component selective responses to plaid motion stimuli in the blowfly visual system. *Journal of Neuroscience*, **32**, 1634-1642 (2012).

Conference Proceedings:

C1. **Krapp H.G.** Optic flow processing for motor control in flying insects. In: Proceedings of the 60th Annual Meeting of the Institute of Navigation, Dayton, Ohio, www.ion.org. (2004)

C2. **Krapp H.G.**: Estimation and control of self-motion and gaze in flying insects. In: Proceedings of the 63th Annual Meeting of the Institute of Navigation, Cambridge, MA, www.ion.org. (2007)

C3. Yue X., Peterson K., **Krapp H.G.**, and Drakakis E.M.: "A Low-Power Low-Distortion Amplifier for Fly Neural Recordings". 4th International Conference on Bioinformatics and Biomedical Engineering (iCBBE), oral presentation, Chengdu, China. Proceedings IEEE, Ei Compendex, ISTP (2010).

C4. Ejaz, N., Tanaka, R.J., **Krapp, H.G.**: Closed-loop performance of a proportional controller for visual stabilization using a fly-robot interface. In: IEEE Int. Conf. Rob. Biomim., pp. 1509–1515 (2011).

C5. Ejaz, N., Tanaka, R.J., **Krapp, HG.**: Static versus adaptive gain control strategy for visio-motor stabilization. In: Biomimetic and Biohybrid Systems, Springer, 7375: pp. 107-119 (2012).

C6. Gremillion G., Galfond M., **Krapp H.G.**, Humbert S.J.: Biomimetic sensing and modeling of the ocelli visual system of flying insects. In: IEEE Int. Conf. Intellegent Robots and Systems (IROS), (2012, accepted).

Book Chapters:

R1. Hengstenberg R., **Krapp H.,** and Hengstenberg B.: Visual sensation of self-motions in the blowfly *Calliphora*. *In*: C. Taddei-Ferretti (ed.) Biocybernetics of Vision: Integrative and Cognitive Processes. Singapore: World Scientific, pp. 41-52, (1998).

R2. Dahmen H., Franz M.O., and **Krapp H.G.**: Extracting ego-motion from optic flow: limits of accuracy and neuronal filters. *In:* (J. M. Zanker and J. Zeil, eds.) Processing visual motion in the real world -- A survey of computational, neural and ecological constraints. Berlin, Heidelberg, New York: Springer Verlag, pp. 143-168, (2001).

R3. **Krapp H.G.** and Wicklein M.: Central processing of visual information in insects. In: Basbaum A.I, Kaneko A., Shepherd G.M., and Westheimer G. (eds) The Senses: A comprehensive reference. Vol. 1, Vision I, Masland R and Albright T.D. (eds.), San Diego, Academic Press, pp. 131-204, (2008)

R4. **Krapp H.G.**, Taylor G.K., and Humbert S.J.: The mode-sensing hypothesis: matching sensors, actuators and flight dynamics. In: Frontiers in Sensing - Biology and Engineering. Srinivasan MV and Barth F (eds.), Springer (2011)

Manuscripts submitted:

Manuscripts in preparation:

O41. Schwyn D.A., Hernandes Heras F.J., Bolliger G., Parsons M.M., Laughlin S.B., Tanaka R.J., and **Krapp H.G.**: Two-degree-of-freedom control of fly compensatory head roll.

O42. Schwyn D.A., Mokso R., Walker S.M., Doube M., Wicklein M., Stampanoni M., Taylor G.K., and **Krapp H.G.:** Gated kHz *in vivo* x-ray microtomography of fast quasi-periodic behaviour.

O43. Baden T. and **Krapp H.G.**: Velocity-invariance of local motion preferences in optic flow processing interneurons.

O44. Humbert S.J., **Krapp H.G.**, and Taylor G.K.: Analysis of *Calliphora* LPTC directional templates.

O45. Wicklein M., Schwyn D.A., Simonsen T.J., Howard L.E., Ball A., Abel R.L., and **Krapp H.G.**: Iodine staining for global and tissue specific contrast enhancement in micro-computed tomography.

Conference abstracts (reviewed & non-reviewed)**:**

A1. **Krapp H.** and Hengstenberg R.: Reliability of a fast method to determine locally the preferred direction of motion sensitive neurons. In: Rhythmogenesis in Neurons and Networks. Eds. N. Elsner, D.W. Richter, Thieme, Stuttgart 1992, 306.

A2. **Krapp H.** and Hengstenberg R.: Representation of specific optical flow fields in lobula plate neurons of the blowfly *Calliphora*. In: Gene - Brain - Behaviour. Eds. N. Elsner, M. Heisenberg, Thieme, Stuttgart 1993, 357.

A3. **Krapp H.**, Hengstenberg B., and Hengstenberg R.: Correspondence of dendritic field structure, receptive field organization, and specific flow patterns in visual interneurons of the blowfly *Calliphora*. In: Proceedings of the 22nd Göttingen Neurobiology Conference, Vol. II. Eds. N. Elsner, H. Breer, Thieme, Stuttgart 1994, 447.

A4. **Krapp H.** and Hengstenberg R.: Comparison between optic flow fields and response fields of visual interneurons in the lobula plate of the blowfly *Calliphora*. In: Proceedings of the 23nd Göttingen Neurobiology Conference, Eds. N. Elsner, R. Menzel, Thieme, Stuttgart 1995, 404.

A5. **Krapp H.** and Hengstenberg R.: Filter neurons for specific optic flow patterns in the fly's visual system. In: Proceedings of the 4th International Congress of Neuroethology, Eds. M. Burrows, T. Matheson, P.L. Newland and H. Schuppe, Thieme, Stuttgart 1995, 264.

A6. Hengstenberg R. and **Krapp H.**: Distribution of roll motion sensitivity in the eyes of *Callophora*: a comparison between neurons and behaviour. In: Proceedings of the 24th Göttingen Neurobiology Conference, Eds. N. Elsner, H.- U. Schnitzler, Thieme, Stuttgart 1996, 349.

A7. Gabbiani F., **Krapp H.**, Koch C. and Laurent G: Biophysical implementation of a multiplication operation in an interneuron of the locust. Soc. Neurosci. Abstr. **23**: 613.17, 1997.

A8. **Krapp H.G.**, Gabbiani F., Koch, C. and Laurent G.: Neuronal Multiplication in the locust visual system. In: Proceeding of the 26th Göttingen Neurobiology Conference, Eds. N. Elsner, R. Wehner, Thieme, Stuttgart 1998, 410.

A9. Franz M.O., Hengstenberg R. and **Krapp H.G.**: VS-neurons as matched filters for self-motion-induced optic flow fields. In: Proceeding of the 26th Göttingen Neurobiology Conference, Eds. N. Elsner, R. Wehner, Thieme, Stuttgart 1998, 419.

A10. Gabbiani F., **Krapp H.**, Koch C. and Laurent G: Computation of object approach by two wide field motion sensitive neurons. In: Soc. Neurosci. Abstr. **24**: 613.17, 1998.

A11. Petrowitz R., **Krapp H.G.**, Dahmen H. and Egelhaaf M.: The distribution of ommatidial axes in *Calliphora erythrocephala* varies with the direction of view. In: Proceeding of the 27th Göttingen Neurobiology Conference, Eds. N. Elsner, U. Eysel, Thieme, Stuttgart 1999, 439.

A12. **Krapp H.G.** and Egelhaaf M.: Local preferred directions of visual wide field neurons and the compound eye geometry of the blowfly *Calliphora erythrocephala*. In: Proceeding of the 27th Göttingen Neurobiology Conference, Eds. N. Elsner, U. Eysel, Thieme, Stuttgart 1999, 440.

A13. Karmeier K., **Krapp H.G.** and Egelhaaf M.: Does the receptive field organization of a blowfly visual interneuron depend on visual experience? In: Proceeding of the 27th

Göttingen Neurobiology Conference, Eds. N. Elsner, U. Eysel, Thieme, Stuttgart 1999, 441.

A14. **Krapp H.G.** and Gabbiani F.: Spatial integration of local motion stimuli by a wide-field looming sensitive neuron. In: Soc. Neurosci. Abstr. **26**: 66.1, 2000.

A15. Egelhaaf M., Petrowitz R., Dahmen H. and **Krapp H.G.**: Adaptation of the compound eye geometry to optic flow processing in the blowfly *Calliphora*. In: Soc. Neurosci. Abstr. **26**: 368.11, 2000.

A16. Gabbiani, F., **Krapp, H.G.**, Koch, C, et al .: Multiplicative computation by a looming-sensitive neuron, 24th Annual International Conference of the Engineering-in-Medicine-and-Biology-Society/Annual Fall Meeting of the Biomedical-Engineering-Society (EMBS 2002 BMES), pp, 1968 – 1969, 2002.

A17. Matheson T., Basu Roy R., Copeland M., **Krapp H.G.** and Rogers S.M.: Plasticity in the visual system of solitarious and gregarious locusts. *Journal of Physiology* **547** P, p91PC, 2003.

A18. Matheson T., **Krapp H.G.** and Rogers S.M.: Neuronal plasticity in the visual system of solitarious and gregarious locusts. *Comparative Biochemistry and Physiology A* **134** (3, suppl), S 73, 2003.

A19. Matheson T., **Krapp H.G.** and Rogers S.M.: Adaptation to lifestyle in the visual system of solitarious and gregarious locusts. In: Proceedings of the 29th Göttingen Neurobiology Conference, Eds. N. Elsner, H. Zimmermann, Thieme, Stuttgart 2003, 483.

A20. Karmeier K., **Krapp H.G.** and Egelhaaf M.: Population coding in the visual system of the blowfly: an experimental and modelling approach. In: Proceedings of the 29th Göttingen Neurobiology Conference, Eds. N. Elsner, H. Zimmermann, Thieme, Stuttgart 2003, 478.

A21. Huston S.J. and **Krapp H.G.**: The visual receptive field of a fly neck motor neuron. In: Proceedings of the 29th Göttingen Neurobiology Conference, Eds. N. Elsner, H. Zimmermann, Thieme, Stuttgart 2003, 483.

A22. Peron S.P., **Krapp H.G.**, Laurent G., and Gabbiani F.: Role of dendritic morphology in the processing of looming stimuli: a compartmental modelling study. Program No. 491.3. 2003 Abstract viewer/Itinerary Planner. Washington, DC: Society for Neuroscience, 2003. Online.

A23. Card G, **Krapp H.G.**, and Laughlin SB: Motion adaptation does not affect the direction tuning of a neuron processing optic flow in the blowfly *Calliphora vicina.* In: University of Cambridge (2004) *Journal of Physiology* **555P** PC129, (2004)

A24. Rogers SM, Harston GWJ, Kilburn-Toppin F, Matheson T, and **Krapp H.G.**: Receptive field organisation of a collision-detecting visual interneurone in solitarious and gregarious locusts. In: University of Cambridge (2004) *Journal of Physiology* **555P** PC130, (2004)

A25. Matheson T, Rogers S, Kilburn-Toppin F, Harston G, and **Krapp H.G.**: Receptive field organization of a collision-detecting visual interneurone in solitarious and gregarious locusts. In: Proceedings of the 7th International Congress of Neuroethology, PO167, (2004)

A26. Huston SJ and **Krapp H.G.**: Visual receptive field organization of sensory and motor neurons in the blowfly. In: Proceedings of the 7th International Congress of Neuroethology, PO168, (2004)

A27. Gabbiani F and **Krapp H.G.**: Receptive field organization of a wide-field, looming sensitive neuron. In: Proceedings of the 7th International Congress of Neuroethology, PO182, (2004)

A28. Gabbiani F and **Krapp H.G.**: Structure and receptive field input organization of a wide-field, looming sensitive neuron. In: Program No. 870.20. 2004 Abstract viewer/Itinerary Planner. Washington, DC: Society for Neuroscience, (2004). Online.

A29. Karmeier K., **Krapp H.G.**, and Egelhaaf M.: Population coding of self-motion in the blowfly visual system. In: Proceedings of the 30th Goettingen Neurobiology Conference. (2005).

A30. **Krapp H.G.** and Huston S.J.: Encoding self-motion: From visual receptive fields to motor neuron response maps. In: Proceeding of the 30th Goettingen Neurobiology Conference. (2005).

A31. Wüstenberg D. and **Krapp H.G.**: Self-motion estimation and flight control in blowflies and locusts: a comparative study. In: Proceeding of the 31st Goettingen Neurobiology Conference (2007).

A32. Parsons M.M., **Krapp H.G.**, and Laughlin S.B.: Multisensory integration: Rotation detection in the visual system of the fly. In: Proceeding of the 31st Goettingen Neurobiology Conference (2007).

A33. Huston S.J. and **Krapp H.G.**: Integration of visual and haltere inputs in fly neck motor neurons. In: Proceedings of the 8th International Congress of Neuroethology, (2007)

A34. Longden K.D. and **Krapp H.G.**: Activity modulation of optic flow processing neurons by an octopamine agonist in the blowfly. In: Proceedings of the 8th International Congress of Neuroethology, (2007)

A35. Rogers S.M., **Krapp H.G.**, and Matheson T.: Compensatory plasticiy at an identified synapse tunes a visuo-motor pathway in the locust. In: Proceedings of the 8th International Congress of Neuroethology, (2007).

A36. Wüstenberg D. and **Krapp H.G.**: Optic flow processing interneurons in flies and locusts. In: Proceedings of the 8th International Congress of Neuroethology, (2007).

A37. Saleem, A, **Krapp, HG**, Schultz, SR, Spike-triggered independent component analysis: A method for receptive field characterization. Society for Neuroscience, Page: 514.10., (2008).

A38. Longden K.D. and **Krapp H.G.**: State-dependent coding properties of optic-flow processing cells in the blowfly visual system. Society for Neuroscience, Page: ., (2008).

A39. Longden K.D. and **Krapp H.G.** Modulation of visual information processing in blowfly Lobula Plate Tangential Cells by an octopamine agonist. In: Proceeding of the 32nd Goettingen Neurobiology Conference (2009).

A40. Ejaz N., Peterson K., and **Krapp H.G.** (2009) A robotic platform to study closed-loop optomotor control in the blowfly. In: Proceeding of the 32nd Goettingen Neurobiology Conference (2009).

A41. Parsons M.M., **Krapp H.G.**, and Laughlin S.B. (2009) Convergence of compound eye and ocellar signals in Lobula Plate Tangential Cells of the blowfly *Calliphora*. In: Proceeding of the 32nd Goettingen Neurobiology Conference (2009).

A42. Longden K.D. and **Krapp H.G.** (2009) Octopaminergic modulation of velocity coding in a blowfly optic flow-processing interneuron. Applied Vision Association Christmas Meeting, Bristol, UK (2009).

A43. Longden K.D., and **Krapp H.G.** (2010) Velocity coding and octopamine in an identified optic flow-processing interneuron of the blowfly. Computational and Systems Neuroscience (COSYNE), 258, Salt Lake City, USA, (2010).

A44. Longden K.D., Saleem A.B., Schultz S.R., and **Krapp H.G.** (2010) Responses to pattern motion of compound stimuli in an identified visual interneuron of the blowfly. 7th Forum of European Neuroscience (FENS), Amsterdam, Holland (2010).

A45. Wicklein M., An J., Selmon A., and **Krapp H.G.** (2010) Comparing the receptive field organization of LPTCs in male and female blowflies. 7th Forum of European Neuroscience (FENS), Amsterdam, Holland (2010).

A46. Longden K.D., Saleem A.B., Schwyn D., Schultz S.R., and **Krapp H.G.** (2010) How blowflies analyse the motion of visual patterns. 9th International Congress of Neuroethology, Salamanca, Spain (2010).

A47. Schwyn D.A., Wicklein M., Klosowski M.M., Doube M., Abel R., and **Krapp H.G.** (2010) Imaging the fly brain using micro-CT. 9th International Congress of Neuroethology, Salamanca, Spain, (2010).

A48. Wicklein M., Schwyn D.A., Abel R.L., Simonsen T. J., and **Krapp H.G.** (2011) Optic lobes in male and female blowflies determined by micro-CT imaging. Ninth Goettingen Meeting of the German Neuroscience Society, Goettingen, Germany, (2011).

A49. Schwyn D.A., Hernández Heras F.J., Bolliger G., Parsons M.M., **Krapp H.G.**, and Tanaka R.J. (2011) Behavioural studies and modelling of gaze stabilization in the blowfly *Calliphora*. Ninth Goettingen Meeting of the German Neuroscience Society, Goettingen, Germany, (2011).

A50. Hardcastle B.J., Schwyn D.A., Longden K.D., Bierig K., Tanaka R.J. and **Krapp H.G.** (2012). Ocellar contributions to gaze control: a behavioural linear systems analysis in the blowfly. *Front. Behav. Neurosci. Conference Abstract: Tenth International Congress of Neuroethology*. doi:10.3389/conf.fnbeh.2012.27.00414, University of Maryland, USA, (2012).

A51. Longden K.D. and **Krapp H.G.** (2012) State-dependent motion vision in walking blowflies. *Tenth International Congress of Neuroethology* (oral presentation), University of Maryland, USA, (2012).

A52. Schwyn D.A., Walker S.M., Mokso R., Wicklein M., Doube M., Stampanoni M., Taylor G.K., and **Krapp H.G.** (2012). Ultra-fast in vivo x-ray microtomography of blowfly wingbeat. Front. Behav. Neurosci. Conference Abstract: Tenth International Congress of Neuroethology. doi: 10.3389/conf.fnbeh.2012.27.00407, University of Maryland, USA, (2012).

A53. Wicklein M., Schwyn D.A., Simonsen T.J., Howard L.E., Ball A., Abel R.L., and **Krapp H.G.** (2012) Radiocontrast micro-CT imaging optimised for differential tissue segmentation in *Calliphora vicina* (blowfly). 15th European Microscopy Congress, Manchester, UK, (2012).

A54. Schwyn D.A., Mokso R., Walker S.M., Wicklein M., Doube M., Müller T., Taylor G.K., Stampanoni M., **Krapp H.G.** (2012) Ultra-fast x-ray microtomography of wing beat in tethered flies. 15th European Microscopy Congress (oral presentation), Manchester, UK, (2012).

Edited Books:

1. **Krapp H.** and Wägenbaur T. (Eds.). Künstliche Paradiese - Virtuelle Realitäten. München: Fink, 1997.
2. **Krapp H.** and Wägenbaur T. (Eds.). Komplexität und Selbstorganisation - Chaos in den Kultur- und Naturwissenschaften. München: Fink, 1997.